GENERAL ZOOLOGY

GUTHRIE · ANDERSON

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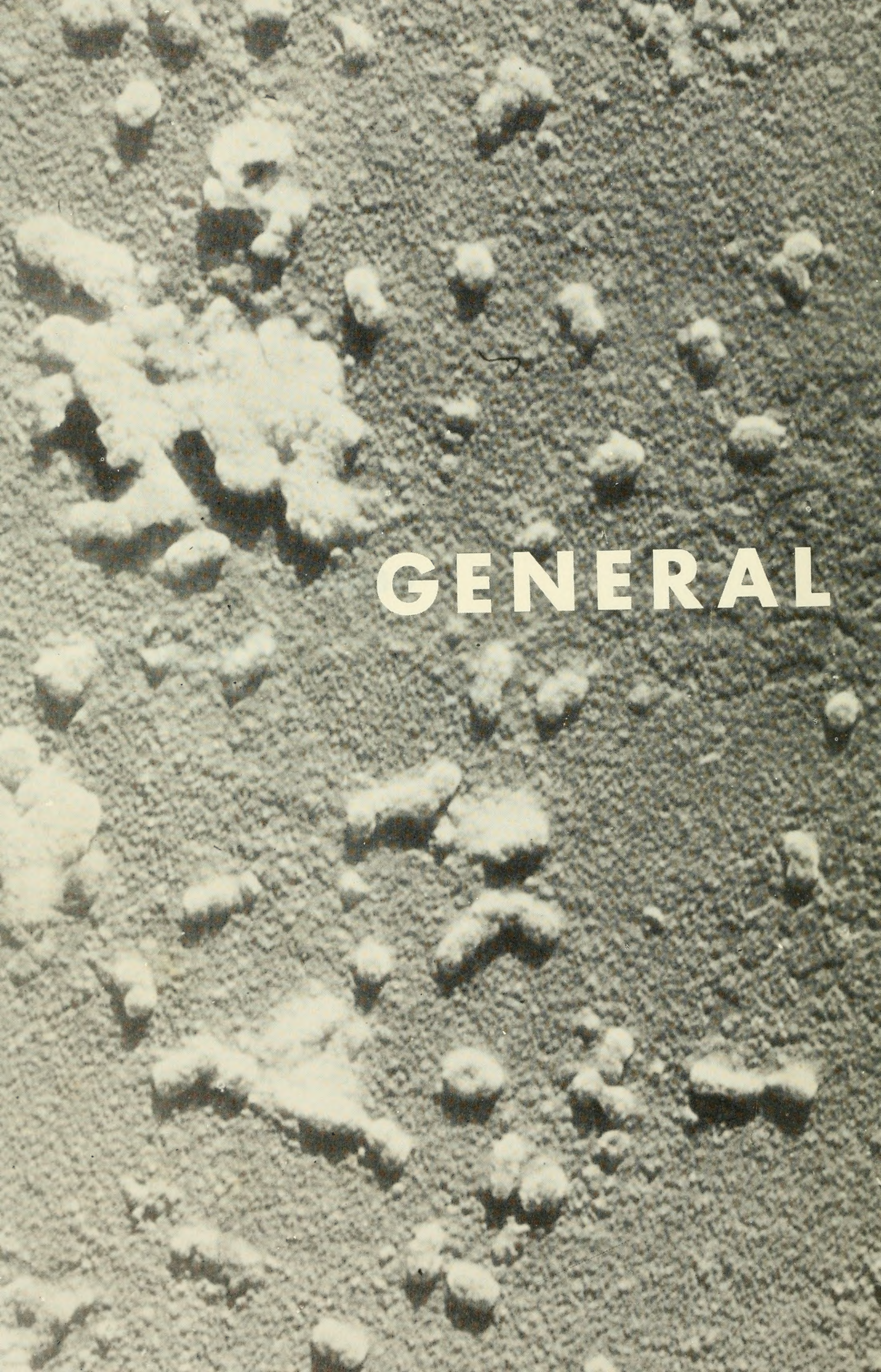
GENERAL
ZOOLOGY



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NEW YORK · JOHN WILEY & SONS, INC.
London

SECOND PRINTING, NOVEMBER, 1961

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Library of Congress Catalog Card Number: 57–13444

Printed in the United States of America

PREFACE

Curtis and Guthrie's *Textbook of General Zoology* has been a standard work in its field through three decades and four editions. The withdrawal of Professor Winterton C. Curtis from active participation in a further revision, together with the rapid development of many areas of zoological knowledge and interpretation, has made the preparation of an essentially new book preferable to the issuance of a fifth edition in the Curtis and Guthrie series. Nevertheless, those familiar with "Curtis and Guthrie" will immediately recognize how much this book owes to its predecessors, in content, organization, and emphasis. In general, we have endeavored to preserve the features of the Curtis and Guthrie texts that have proved successful in teaching practice and to revise and amplify the parts that progress in zoology has made inadequate.

This is not an easy, superficial book. We are convinced that giving the student an insight into the great depth and richness of zoology may awaken his interest and so fire his imagination and curiosity that he will find the subject worthy of further study. Even if he is a terminal student, contemplating no studies in zoology beyond his introductory course, leading him into some of the more profound aspects of the subject will make his limited experience more rewarding. His textbook should not be one in which he merely performs assigned readings; he should have a book he can read with enjoyment, one that gives him a broad foundation and background for the sometimes narrow and necessarily restricted view of zoology which he glimpses in classroom and laboratory. On the other hand, there are limits to the amount of factual information and learned terminology to which students should be subjected in introductory textbooks.

We do not believe, as some zoologists do, that emphasis on anatomy, and on the phylogenetic relationships which can often be inferred from structural similarities, constitutes an outmoded approach to zoology. Although the most dynamic recent advances have stemmed from physiological studies, an understanding of structure is prerequisite to an appreciation of the functions of organisms. Our objective has been to write a book in which functional aspects are emphasized, but in which they are made coherent and intelligible by a full exposition of the anatomical features involved. Further, we have attempted to combine factual information with the interpretations and conclusions which the facts justify and which give point and meaning to the facts as presented.

The approach of the present work, like that of the Curtis and Guthrie series, is to begin with the vertebrate type of organization, introducing the student to various aspects of structure and function in vertebrates and then proceeding to a stepwise consideration of how the vertebrate organization developed through evolution. The early chapters, although generally oriented toward the vertebrates, deal broadly and comparatively with such subjects as cellular structure and function and the universal aspects of metabolism and responsiveness. Accordingly, these chapters furnish an introduction to principles that apply throughout the Animal Kingdom.

The organization of this book has been made flexible enough to permit different manners of presentation. A teacher may elect to follow the order of the chapters, or to begin with classification (Chapter 7), study the invertebrate groups, and then return to the vertebrates. Depending on the organization of his course, the teacher must decide when the general chapters—those dealing with classification, heredity, ecology, and evolution—can be most appropriately integrated. The broadly comparative survey of invertebrate organ systems and vital functions (Chapter 17) may be particularly useful in courses taking formal notice of only a few of the invertebrate groups and will serve as a basis for broad comparisons if only vertebrates are studied in detail.

To those teachers who favor a man-centered approach to zoology, the extended treatment given the invertebrate groups in this book may seem unwarranted. To us it appears that since the vast majority of animals are invertebrates, to ignore them is to lose sight of man's relation to the animal world and of the teeming mass of more primitive types from which the vertebrates have so recently emerged. The chapters on invertebrate phyla do not merely form a systematic survey of the Animal Kingdom but present a careful analysis of each group, its significant structural and functional aspects, and its place in phylogeny. The unifying theme of this section of the book is the progression of levels of organization through evolution.

The several chapters discussing the representative types of animals regularly include remarks on their activities and habitat relations. In addition, a separate chapter has been devoted to ecology. Here we discuss the short-range and long-range interactions between animals and their environments, the specific effects of many environmental factors in determining the survival and distribution of animals, and the concepts of competition and the balance of nature. This material is, in part, a preparation for the following chapter in which the role of the environment in evolutionary change is discussed. We hope that this chapter on ecology fills the gap reported by many who have used the Curtis and Guthrie textbooks.

A major problem on which there is little agreement among teachers of zoology has been aptly termed "the chemistry dilemma." Students of beginning zoology commonly have little if any background in chemistry, yet many extremely significant aspects of zoology cannot be adequately presented without reference to biochemical concepts. Chief among these are the mechanisms whereby foods are utilized in the body and the pathways through which energy is obtained, transformed, and utilized in cells. In no area of biological science have more rapid advances been made during the past decade than in the elucidation of the complicated enzyme systems of cellular metabolism. To discuss these phenomena in the vague terms customary in introductory textbooks is to skirt around the central fact of life itself. The presentation provided in this book is as simple and straightforward as it can be made and is supplemented by a diagram showing the interrelations of the various enzyme systems. The subject is no more difficult to understand than, for example, the sequence of events in digestion or the life cycles of many parasites. Perhaps only a few students will become aware of the deeper implications of this study, but all should acquire more than just a vague idea of the pathways of energy utilization in cells. The mechanisms of cellular metabolism will undoubtedly become a standard feature of introductory zoology, just as all achievements of advanced research are eventually reflected in introductory teaching.

Although many areas of zoology are developing so rapidly that no textbook can be expected to remain completely up to date for more than a few months, we have incorporated the recent discoveries that have come to our attention. Thus, in the section describing the morphology of cells, full use has been made of the results obtained by thin-sectioning techniques and electron microscopy. A surprisingly well-developed nerve net has been reported in sponges, suggesting the necessity of revising the classical concept of coordination in these primitive metazoans. The discoveries relating to hormonal integration in arthropods have been incorporated at several points. But beginning students are often stimulated to eager interest by realizing that much is yet to be discovered in zoology; accordingly, we have consistently noted significant gaps in knowledge of structure, function, and life cycles in animals.

For the most part, new illustrations have been prepared for this book. Some excellent figures from the fourth edition of the Curtis and Guthrie text have been retained, usually after redrawing and modification. Aside from original drawings and photographs, there can be no better source for textbook illustrations than figures appearing in the original scientific articles, handbooks, or monographs in which a discovery is reported or some special feature of an animal described. Therefore, many of our illustrations have been taken from such sources, modified as necessary for our purposes. In each case a full reference to the source is given following the legend so that the teacher or the interested student may consult the original article. The large majority of line drawings were prepared by Bente Starcke King, to whom we are much indebted for her faithful and talented services. Additional drawings were made by Mary Guerriere Loomis and Evelyn J. Erickson; preliminary lettering in some charts was the work of Asad Isaf. To all of these contributors we express our appreciation.

The senior author has been responsible for the preparation of Chapters 1 through 6, and the junior author for the remainder of the book. Each has profited greatly from the rigorous criticisms and constructive suggestions of the other, and both are content to be held jointly responsible for errors or omissions in any part of the book. It is our hope that past users of the Curtis and Guthrie texts will agree that the innovations introduced in this new book constitute improvements and add to its usefulness.

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Detroit, Michigan
Ithaca, New York
October 1957

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GENERAL

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CHAPTER 1

INTRODUCTION

This is your introduction to a book which is written to help you gain an understanding of the science of animal life. Perhaps you are wondering whether you need or want this information and why such subject matter forms a part of a college curriculum. Your course of study will usually include three kinds of material – (1) tool subjects, such as composition and speech training in various languages, which aid you in gathering or imparting ideas, or mathematics and logic, which offer training in reasoning and the use of abstract ideas; (2) technical subjects in which you can acquire the professional training that will aid you in earning a livelihood when college days are over; and (3) cultural subjects in which you become better acquainted with your social heritage, the rich background of man's artistic contributions in literature, music, and the arts and his intellectual attainments in the fields of religion, philosophy, and science. In this book you will find a general survey of the facts and theories that constitute a particular branch of science.

So many of our activities are made easier, or are indeed even made possible, by the applications of science that it is sometimes said we live in an age of science. The automobile and airplane, radio and television are accepted parts of our lives, carrying us literally and figuratively over all the world, increasing our information, and adding to the pleasure of our existence. Most of us probably consider inevitable and not particularly surprising the widespread use of atom-powered ships at sea and in the air, and of solar batteries to harness energy from the sun, which we are told to expect in the not too distant future. So accustomed are we to the continued march of marvels in our age that we may forget our indebtedness to the basic knowledge of nature which has been applied in such countless ways for our benefit.

From agriculture, as from industry, we receive indirectly the fruits of science. Crop rotation as well as erosion control save the soil. Domesticated animals are improved with respect to egg or milk production. Disease-resistant grains are found, and new types of fruits and vegetables are propagated. New chemicals are introduced to help in the never-ending war with the enemies of our food supply—insects, fungi, weeds. The experiment station is a recognized part of colleges of agriculture throughout our country. Long-range weather forecasting now benefits both rural and urban dwellers, whether in planting and harvesting crops or in planning recreational activities. But the national problem of water shortage seems far from solution, a challenge to the accumulation and application of necessary information.

The life span of man has been increased by the applications of science which we find in the practice of medicine. Against polluted foods and against the spread of disease we have a measure of protection undreamed of a hundred years ago. No longer do plagues bring terror to a district, although diseases such as the common cold and cancer remain unconquered. Preventive measures against smallpox and typhoid fever are almost universally used, and inoculations to prevent other diseases and to aid in their cure have a wide acceptance. Antibiotics, such as penicillin and aureomycin, are notable contributions of science to the control of disease. The study of many problems of public health are discussed frequently in the public press and are excellent illustrations of the way in which basic scientific investigation is being applied in the attempt to make our health more secure.

Many other examples of applied science will occur to you. What, exactly, is science? If you consult a dictionary, you will find that the word science is derived from the Latin *scientia*, meaning knowledge. In modern usage, science is knowledge gained by observation and reasoning; it is factual information, correlated and systematized. One of the most important things that any student of elementary science can learn is what is meant by the **method of science.** This method is not the private property of scientists but has wide application for anyone who will understand and use it.

The knowledge we call science is based upon facts. A **fact** is the real state of things, as distinguished from a belief. How do we determine what is a fact? By observation, by the use of our sense organs. Science begins with sense perceptions. We see that water changes to vapor as it boils; we feel the increasing temperature of a wire held in a flame; we hear the call of a bird. Man has made instruments of measurement in order to record his observations quantitatively and to be able to compare them with those of other observers. It is not profitable to argue about where the corn grows tallest or the buildings are highest because both corn and buildings can be measured, and argument fails to alter facts. The point to understand is that, whatever the branch of natural science, observations on things are its raw materials. Wherever possible these observations are recorded quantitatively—things are counted or measured.

The scientist is not satisfied with the things nature shows him in her own way. His curiosity is aroused by what she reveals, and he wants to know more. Therefore he tries to think of a way to learn her secrets—he plans an **experiment.** Naturalists before the time of Gregor Mendel had observed that, when plants which differed in certain characteristics were cross-pollinated, both types of plant reappeared in subsequent generations. Mendel planned experiments in which he used plants that he had raised for several generations and knew to be true breeding (p. 175). He made crosses between plants that differed in only one respect, such as color of flower, length of stem, or color of seed. When the offspring of these crosses appeared, he classified them and recorded the number of each kind. After several years Mendel had a considerable number of recorded facts about the occurrence of these different plant characters in the offspring of successive generations. He had the first accurate data about the course of inheritance.

The painstaking accumulation of **data,** the recording of facts, is only the beginning of science. What do the facts mean; do they have any relation to other recorded facts? Mendel studied his data in order to find the meaning of what he had observed during his experiments. He found that he could explain these facts of heredity by assuming the existence of units of inheritance which behaved in definite ways. In other words, he formulated in his thinking a **hypothesis** which correlated the facts he had observed. A hypothesis is not regarded as a final explanation. It is subjected to the most rigorous tests that can be devised. If it stands these tests, it is more highly regarded as a correct generalization, one which will render understandable all facts similar to those upon which it is based and one by means of which predictions can be made. Thus Mendel's generalizations about heredity have been confirmed in a great variety of crosses and have, therefore, changed in status from hypotheses to **laws** or **principles** of heredity. If we are acquainted with these principles, we can predict what will happen when breeding experiments are performed.

The method of science, then, uses the facts of nature as they can be verified by all competent or trained observers. When these facts are recorded, they are analyzed by logical processes of thought, and a generalization which correlates the specific, separate facts is proposed. This generalization, or hypothesis, is then tested and if found unsatisfactory is discarded. When a hypothesis, or theory, has been refined until it seems to be entirely adequate to explain a large body of facts and to serve as a basis for prediction, it becomes known as a principle or law. But no scientific principle is beyond criticism; if new facts that cannot be correlated by its statement are discovered, the principle must be revised or discarded.

Science is a slave to the real state of things; truth is its taskmaster. And, because scientists are human beings, they must be constantly on guard lest prejudice or other emotional vices creep unrecognized into the path of rational thinking. The material that is presented to you in this book has been gathered by hundreds of men and women trained in the techniques of observation and logical thinking. It is necessarily summarized without reference, in most cases, to names or personalities, but it is hoped that your teachers will tell you at times some of the fascinating human-interest stories about scientists and their work.

What can you as an individual in a democratic society gain by an understanding of the method of science? You will find that the method of science leads to the accumulation of exact information which is subject to confirmation by any competent observer. It will perhaps occur to you that this accuracy of basic information is responsible for the steady progress of science and the reliability of its applications. Propaganda, or attempted distortion of facts, is no part of scientific procedure. What would be the result of the application of the scientific method to the problems of social organization, government, and international relations? What would happen if some of the "diseases" of our social system were analyzed in an unprejudiced way by competent specialists who were then permitted to conduct carefully planned experiments in an effort to determine what treatment was most effective? We live in an age of science, surrounded by the material benefits of sound observational and experimental practices. Will the time come when we extend these sound practices in the obvious way and reap their benefits in a greater social security? It will come when great numbers of you take an understanding of the scientific method from your college classrooms and apply it to the problems which confront you as citizens in a democracy.

It is sometimes said that science is an enemy of society. When through the utilization of some scientific principle it becomes possible to make something by means of machinery instead of by human hands and then control the machines by means of other mechanical devices, workmen lose their jobs. And when improvements in methods occur simultaneously in many fields, technological unemployment may become an important social problem. Does this result suggest that machines should not be made, that science should not be applied? No, continuing advances in new directions open many new jobs to replace the ones taken over by machines. The slaughter of man in automobile traffic is one of the more appalling aspects of modern life. Would you be willing to argue that automobiles should never have been built? Advances in the chemistry of cellulose, a compound present in plants and abundantly available for use, have made possible the manufacture of artificial textiles and dozens of articles in daily use, as well as the development of high explosives. Because men have used these explosives to blow one another to bits, would you say that the chemistry of cellulose should never have been studied? Your generation will see either the solution of the problem of controlling the energy which scientists have released by techniques of atomic fission and fusion, or the end of civilization as your parents knew it. Does anyone argue, in his fear of disaster from the unscrupulous use of atom and hydrogen bombs, that scientists should not have tried to unlock these storehouses of energy which can be applied with almost unlimited benefits to mankind? No, science is not an enemy of society except as man perverts its contributions. And there are perversions less conspicuous than those mentioned but none the less dangerous. In much advertising we find a completely unwarranted use of "science says" or "science shows" to lend support to fantastic statements. The thoughtful person will ponder these matters.

If, as we have said, science is the slave of truth, and if objectively verifiable fact is the currency of science, it is obvious that science and its distinctive methods cannot operate except on a basis of fact. Human experience encompasses, of course, areas in which beliefs can only be based upon faith, and such beliefs cannot, by their nature, be subjected to rigorous scientific verification. Human knowledge, then, is founded partly on fact and partly on faith, but it has a fundamental unity which has tended to become obscured through the ages of human experience. The Greek philosophers were, literally, lovers of wisdom, and their thoughtful discussions ranged through man's physical, social, and spiritual problems. The dissipation of this unity has resulted partly from the vast increase in knowledge which has come about because of the insatiable thirst of some men for detailed information about a seemingly endless number of facets of their environment. But poets, artists, scholars in all fields, and even spiritual leaders have contributed to this loss of unity, along with the scientists. Today, higher education is intended to help prepare each student to resynthesize for himself a total awareness of man in his relation to the universe—a unity of understanding blended of fact and faith that has been lost through the centuries.

Before we go farther, you should perhaps be told that you will find many words that will be new to you. Each branch of science has its special vocabulary, just as every type of industry or sport has its own list of technical terms. These words will be defined the first time they are used, and many of them will be found in the glossary at the end of this book. Learn to spell these words, to understand their meanings, and to use them correctly. You will enrich your vocabulary as a cultured individual, and you will help yourself in learning the material that is presented in this book. You learn a new vocabulary every time you learn a new game or become a "fan" of some different sport. Be cooperative; help yourself and your teacher by learning the vocabulary of biological science.

If your parents used a forerunner of this textbook when they studied zoology in college, they will probably be quite astonished by the many new words they see in scanning this edition. The growth of science in recent decades has been phenomenal, and zoology has shared in this growth. In zoology, as in other areas of science, new techniques and instrumentation have come into use, new discoveries have been made, new insights have revealed new concepts. Gradually, whole new fields of knowledge have developed; many of these have become, in the course of time, recognized subdivisions of the general subject. It should be emphasized, however, that such subdivisions, or fields of specialization, have come into being not because of any fundamental discontinuities in the subject itself; there is, as we have said, a fundamental unity in all human knowledge. In fact, a conspicuous feature of the growth of many special fields in zoology, for example, has been the realization that the solution of zoological problems requires the use of techniques and concepts of physics and chemistry. The compartmentalization of knowledge into subject fields has come about largely because, in the sciences particularly, information has increased so rapidly that it has become impossible for any individual to keep abreast of developments in more than a relatively limited area of knowledge. Thus, he becomes a specialist in one or a few related fields; and, in the words of a current quip, he spends his life learning more and more about less and less. No specialist, however, pursues this course to the obvious end of knowing everything about nothing.

In beginning to tell you what this book is about, we must set forth the names and provinces of a number of scientific fields; but you must remember that these divisions are recognized only for convenience. Science is knowledge gained by observing and reasoning, and it is divided on the basis of the source of the observations. Thus, the **social sciences** deal with knowledge gained by the study of man in his social relations. In the **natural sciences,** on the other hand, we find two different types of information. First, in the **physical sciences,** such as astronomy, physics, chemistry, and geology, knowledge of man's non-living surroundings is accumulated. Second, in the **biological sciences,** botany, zoology, and psychology, knowledge of living things is sought.

Biology, then, is the science of living things, both plants and animals.

Botany is the science of plant life. **Zoology** is the science of animal life. We observe different aspects of animal life, and each branch of zoology has its name. When we study the structure of animals or find the parts of which they are composed, we call our knowledge **morphology**. **Physiology** is the study of function, or the ways in which the parts of animals work. **Embryology** is the study of the development of the individual, the changes through which a fertilized egg passes from its embryonic stages to the adult form. **Genetics** is the study of heredity and variation. **Taxonomy** is the study of the classification of animals into groups on the basis of structural similarity. **Ecology** is the study of animals in relation to both the living and the non-living constituents of their environments, or surroundings. **Zoogeography** is the study of animal distribution on the earth's surface at any particular period. **Paleontology** is the study of animal distribution on the earth's surface from the distant past to the present in successive geologic periods; this includes the study of the structure of fossil remains of extinct animals and comparison among those found at different periods.

Two major generalizations have been formulated and verified on the basis of observations and experiments in these several subdivisions of biological science. These are the **Cell Theory** and the **Theory of Organic Evolution**. The first of these is both a light illuminating major areas of biological information and a tool for extending the boundaries of these areas. In the following chapter we shall begin to show you how important the Cell Theory is in understanding any single living individual. On the other hand, the second of the great generalizations of biological science, the Theory of Organic Evolution, brings together in a pattern of unity and continuity the varying expressions of life in the countless thousands of kinds of individuals. When you have had the opportunity to learn about some of these many groups of animals, the Theory of Organic Evolution will be discussed in the final chapter of this book.

Earlier in this chapter science was listed as a cultural subject. It is as such that we wish to present the science of zoology. The theories of biology have made a deep impression on man's thinking, his literature, and his social philosophy. No better illustration can be cited than the Theory of Organic Evolution. Laws have been passed to suppress it, churchmen have debated its merits, and wars have been justified by its use. In most cases exact information about the material correlated by this theory has not been used by those who would discredit it. They have not understood that the test of a theory is a very simple one. It must explain facts which can be observed. If any theory does that, no legislation, no debate, and no misuse can contribute to its downfall. With the information to be gained from this book you will be in a better position to accept or reject on their merits many ideas about biology with which you will come in contact outside the classroom. You will be more competent to judge the soundness of social legislation supposedly grounded in biological principles. And, if you are going to be a farmer or a physician, what you learn here will be found basic to the applied sciences which are to be your techniques. No matter what your post-college days hold, we hope that your course in zoology will serve to link man's past attainments in this field of knowledge with the progress you can follow year by year throughout your life.

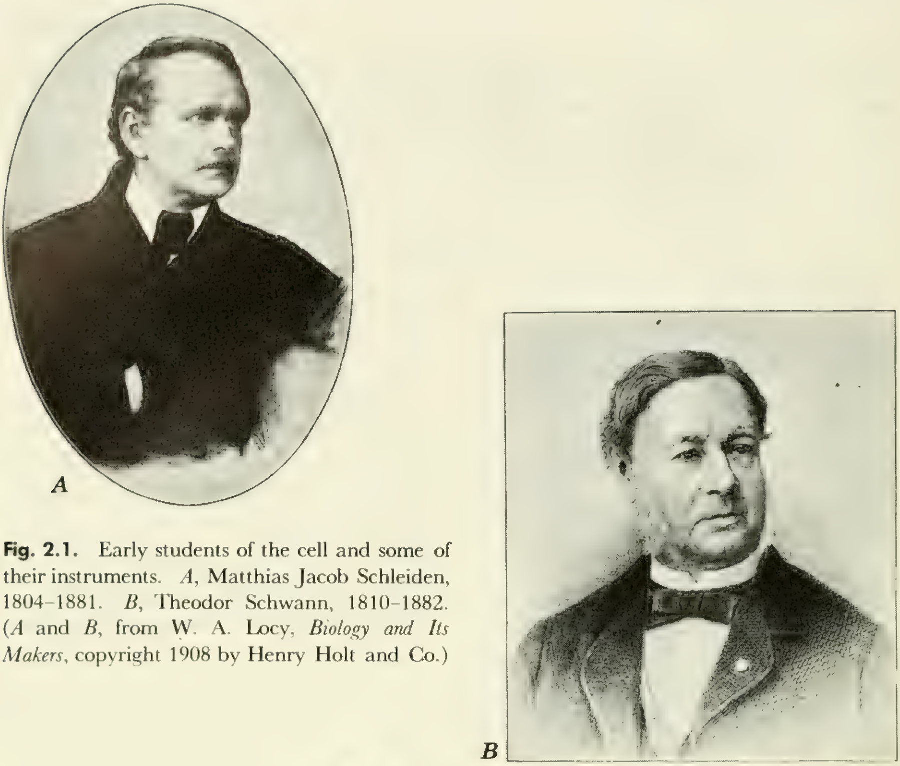
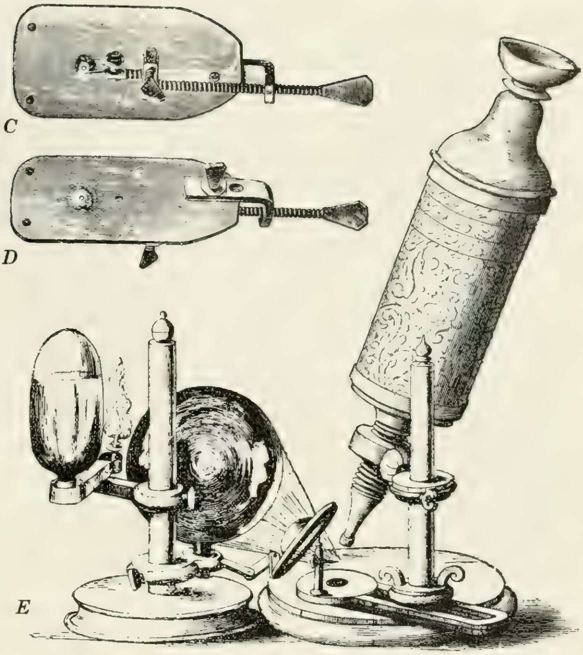


Fig. 2.1. Early students of the cell and some of their instruments. *A*, Matthias Jacob Schleiden, 1804–1881. *B*, Theodor Schwann, 1810–1882. (*A* and *B*, from W. A. Locy, *Biology and Its Makers*, copyright 1908 by Henry Holt and Co.)

CHAPTER 2 STRUCTURE

Animals may be large or small, live in water or on land, lay eggs or give birth to their young. Some have backbones as man has and are known as vertebrates; others, lacking such a support, are called invertebrates. There are more than a million kinds of animals but all of them have many common features. We shall find, for example, that every animal is composed of one or more cells, as the units of structure in living organisms are called; there are unicellular animals and multicellular animals. In the multicellular animals, the cells are not all alike. Instead, there are a number of different kinds of cells, each type occurring in a group known as a tissue; the details of cells and tissues are not visible to the unaided eye. The tissues are further grouped to form organs which can be separated by dissection.

Animals, whether single-celled or many-celled, must obtain food and oxygen from their surroundings, or environment, in order to live. With very few exceptions, animals cannot make their food. Each individual must break down, or digest, food which he has obtained from some other animal or plant



C and *D*, different views of the microscope used by Antony van Leeuwenhoek (cf. p. 140) about 1673. *E*, the compound microscope used by Robert Hooke (cf. p. 11) about 1665, showing method of illumination. (*C*, *D*, and *E*, from W. B. Carpenter, *The Microscope and Its Revelations*, copyright 1891 by J. and A. Churchill, reprinted by permission.)

AND ACTIVITIES OF CELLS

and rework it to satisfy his own needs. The more highly organized animals have organs which are responsible for digesting their food, for obtaining their oxygen, for eliminating undesirable materials, for transferring substances from one part of the body to another, and for integrating all the activities of the body. An understanding of these functions rests on an understanding of the cells that make up the tissues and organs. In this chapter we are going to discuss the structure and activities that cells of all animals, whether simple or complex, have in common.

The Cell Theory

The discovery of cells was made possible by the use of the microscope, which was invented about 1591 but was not utilized in scientific studies until about 1650. Robert Hooke, one of the early English microscopists, discovered that cork is composed of small spaces surrounded by firm walls, and in 1665 he named these compartments **cells.** The development of microscopic instruments was very slow, and it was not until 1831 that Robert Brown observed in certain plant structures that each cell contains a small body, which he called the **nucleus.** In 1838 Schleiden, a German botanist, proposed the interpretation that cells are the units of structure in plants; and Schwann, a German zoologist, extended this conception to the structure of animals in 1839 (Fig. 2.1). This was the first formulation of the **Cell Theory.** The founders of this theory and other biologists of that time believed that the walls surrounding plant cells were the essential parts of these units. The contents of cells had been observed but were regarded as unimportant or as waste products. Purkinje in 1840 and von Mohl in 1846 gave the name **protoplasm** to the cell contents. Through a series of researches it became apparent that protoplasm was the essential part of cells; walls were found only around plant cells. Likewise, a nucleus was found to be present in almost all types of cells, and a cell came to be defined as a mass of protoplasm containing a nucleus.

As knowledge increased, it was ascertained that in certain parts of the animal much non-cellular material lies between cells. This material, examples of which will be given later, was shown to be produced by cells, and the Cell Theory was modified to state that organisms are composed of structural units, called cells, and of cell products. Further study of animals with reference to their activities has revealed the fact that all physiological processes must be understood in terms of the functions of cells; that is, the cell is the unit of function. The Cell Theory has, therefore, been extended and confirmed, and it now stands as one of the fundamental generalizations of biological science. A complete statement of this unifying conception of biology would be that all living organisms are composed of cells, the units of structure and function, and of cell products. In complex organisms these units are not independent but are coordinated by their own activities, so that the animal as a whole may also be regarded as a unit. This obvious fact of interrelation among the cells of an individual is sometimes emphasized in what is called the **Organismal Theory.** In the final analysis the organism is regarded as a protoplasmic unit according to this theory, and there is no essential difference between it and the modern interpretation of the Cell Theory, which is much easier to use in understanding the structure and function of an animal.

Distinguishing Capacities of Living Organisms

Living organisms differ from lifeless things in three fundamental respects. These distinguishing capacities are metabolism, responsiveness, and reproduction.

Metabolism is the capacity as a result of which cellular constituents are built up and destroyed in such a way that the organism lives. The chemical reactions occurring during metabolism can be grouped under the headings anabolism and catabolism. **Anabolism** includes those reactions by which suitable substances are built up or synthesized into the constituent compounds of cells. **Catabolism** includes the destructive reactions which occur in cells, bringing about the release of energy, together with the production of heat and certain waste products. **Growth**, or increase in cellular volume, occurs in living organisms when anabolism occurs at a more rapid rate than catabolism. Organisms grow from within; they differ in this respect from inorganic crystals, which grow by the process of accretion, the deposition of additional material on the surface of that already present. Metabolic reactions are catalyzed by the enzymes (p. 28) typical of living cells.

Responsiveness is the capacity as a result of which cells respond to stimuli, or changes in their environment. It is on this characteristic that the interactions not only among the various constituents of a cell but also among the different cells and systems of an individual depend. It is well known that nonliving things react in certain definite ways to changes in their surroundings, as when metals undergo particular amounts of contraction for particular decreases in temperature. The reactions of living organisms, however, involve both chemical and physical factors and are so much more complicated as to be distinctive.

Reproduction is the capacity as a result of which certain cells of an organism can become detached and, either alone or after union with cells of another organism of the same kind, can give rise to a new individual capable of becoming in all essential respects like the parent or parents. Nothing comparable with reproduction is known to occur among inanimate objects. The capacities of metabolism and responsiveness enable the individual organism to maintain itself as a living unit. Maintenance of the species is made possible as a result of the capacity of reproduction.

Methods of Studying Cells

It has been stated that discovery of the fact that living animals and plants are composed of cells containing nuclei was made possible by the invention and improvement of what we now call the compound microscope or **light microscope**. Increase in knowledge of the structure of the cell and its parts has gone hand in hand with improvements in techniques for preparing the cells for study and in instruments for magnifying small objects.

From an early date, students of the cell found that rapid killing or so-called **fixation of tissues**, followed by other special procedures, made it possible to slice them in thin sections. This increased the amount of light which could pass through them and facilitated microscopic examination. **Staining** of such thin sections adherent to glass slides can be accomplished with dyes that have selective affinities for different parts of the cell. Skill in grinding and assembling lenses from the finest glass greatly increased the magnification and

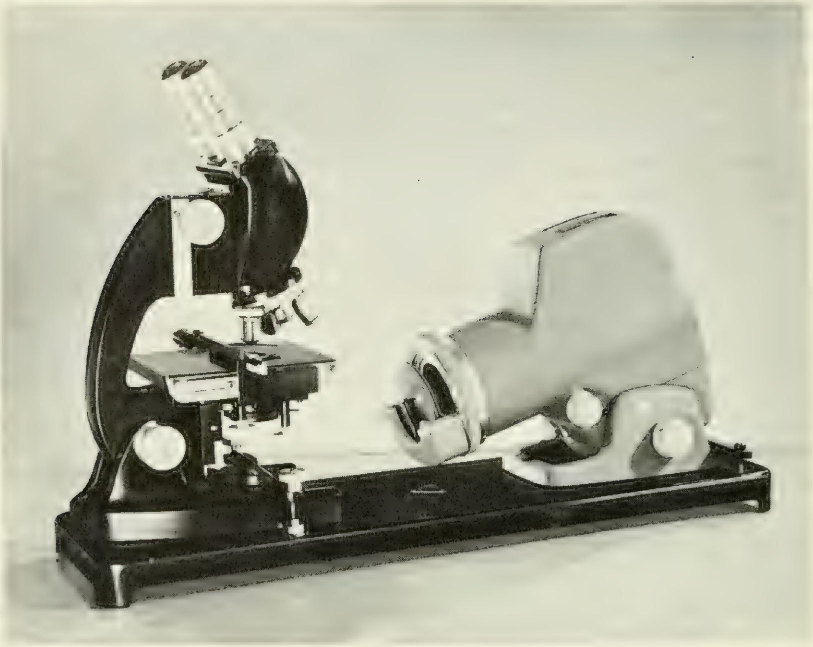


Fig. 2.2. Light microscope with illuminator. (Courtesy Bausch and Lomb Optical Co.)

the distinctness of images seen with the compound microscope in these stained cells (Fig. 2.2).

It was found, however, that in some cases the fixation and staining produced undesirable modification of cell structures as compared with living cells. On the other hand, even when living cells were isolated so that adequate light was transmitted for microscopic examination, it was extremely difficult to distinguish the exact limits of fine structures because of the similarity of their optical densities. It was like trying to see glass beads in a vial of cedar wood oil. The introduction of new diaphragms and lenses into the optical system of the microscope made it possible to gain sharper contrast between cellular parts hitherto virtually indistinguishable. Light microscopes equipped with such diaphragms and lenses are known as **phase-contrast microscopes** and were first sold in this country about 1944.

Even under the best conditions the smallest object that can be seen clearly with the light microscope is 0.25 micron (μ) or 2500 angstrom units (A.) in diameter. A micron is 0.001 mm.; an angstrom unit is 0.0001 μ. An entirely different kind of microscope, known as the **electron microscope**, makes it possible to identify objects as small as 10 A. in diameter (Figs. 2.3 and 2.4); this instrument was first available commercially in this country in 1941. In the electron microscope, the smallest of which is many times larger than a light microscope, a stream of electrons from a heated tungsten filament is directed, in a vacuum, through an extremely thin slice of tissue onto a photographic plate where the magnified image of the cell can be recorded. The preparation of tissue slices no more than 0.1μ in thickness requires great skill in microtechnique; sections for study with the light microscope range from 3 to 8μ in thickness. Prints of the photographic negative of the image are usually enlarged so that cellular structures magnified hundreds of thousands of diameters are available for study in an electron micrograph.

The techniques discussed so far made possible the accumulation of information about the parts of cells as they exist together in their normal relationships. Additional knowledge of cells has come from separating these parts in order to establish their integrity and to seek to determine their functions. In the technique of **microdissection**, very fine glass needles are mechanically manipulated to separate parts of cells with great precision under the light microscope; movements of the delicate instruments can be controlled over a distance as short as 0.5 mμ. With micropipettes, parts can be sucked out of one cell and transferred to another. The more drastic techniques of **cell fractionation** involve grinding or homogenizing the cells and then centrifuging the resultant conglomerate. Particles of different densities are aggregated in

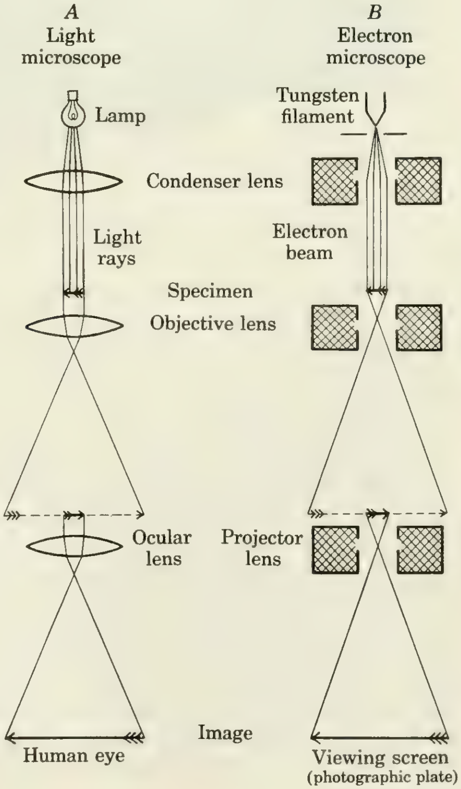

A
Light microscope
B
Electron microscope
Lamp
Tungsten filament
Condenser lens
Light rays
Electron beam
Specimen
Objective lens
Ocular lens
Projector lens
Image
Human eye
Viewing screen (photographic plate)

Fig. 2.3. Diagrams of light and electron microscopes to suggest similarity. The lenses in the light microscope are glass. In the electron microscope, the lenses are magnetic fields, the strength of which can be varied in order to focus the image on the viewing screen. This can be turned aside to permit recording of the image on the photographic plate. (Courtesy Radio Corporation of America.)

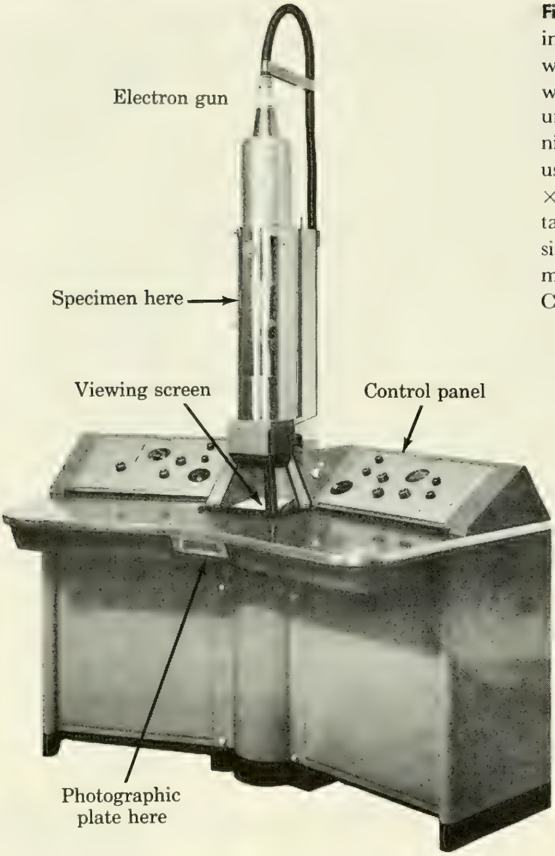


Fig. 2.4. Electron microscope. This instrument is almost 8 feet high and weighs about 1400 pounds. Objects with a diameter of only 20 angstrom units can be resolved. Initial magnification range is ×1400–30,000; useful photographic enlargements of ×200,000 magnification can be obtained. With a magnification of this size, a dime would be more than 2 miles in diameter. (Courtesy Radio Corporation of America.)

separate layers in a centrifuge tube. These layers can then be selectively removed and relatively uniform groups of cell parts obtained. **Biochemical techniques** are used in an effort to determine the chemical composition of such isolated cell parts and to investigate their function in the life of the cell.

Cells and their parts are usually studied as taken from their normal positions in the organs of an animal. However, information about the capabilities of individual cells or groups of them can be increased by growing cells removed from the control of the coordinating mechanisms of the organism. Cells, wherever they are, must have their basic requirements for life satisfied. They must be handled with sterile techniques, so that they are not contaminated with microorganisms, be able to obtain essential nutrients and oxygen, and be kept moist. They must also be incubated at their normal temperatures and have the waste products of their metabolism removed. When the technique of **tissue culture** is used, small bits of tissue are removed from an organism and placed in tubes or flasks in which a nutrient solution bathes them as the containers rotate in an incubator. Cells migrate out from the original bit of tissue and grow as thin sheets in which their activities can be studied. In **organ culture** very small organs are grown (Fig. 2.5). The reactions of their cells can be studied as they exist normally with reference to their neighbors in the organ but apart from the normal hormonal or nervous control of the body (see Chap. 4). In both tissue and organ culture a group of normally associated cells is removed for growth outside the body. **Dissociation of cells** can be accomplished by gentle techniques that digest the material cementing the cells together, much as mortar might be removed from a brick wall to recover the individual bricks. Such dissociated cells can be studied as spread on glass slides or as grown by methods of tissue and organ culture.

A Composite Cell

A cell may be correctly defined, in a general way, as a mass of protoplasm containing a nucleus. Certain cells, however, notably the red blood cells of mammals, lose their nuclei before they enter the blood vessels; others, such as striated muscle cells, contain many nuclei. If the definition is to hold for all cases, it must be modified to state that a cell is a mass of protoplasm which contains one or more nuclei at some time in its life. This statement, together with the definition of a cell as the unit of structure and function, is of fundamental importance in the further consideration of cells. Structurally, cells are divided into two main parts, the cytosome, or cell body, and the nucleus. In the following account these parts will be discussed as they occur in what may be called a composite cell which is not dividing; that is, parts that can be identified in many different kinds of cells are described in a single cell. We shall explore this cell from the outside inward.

The **cytosome** of an animal cell contains what is commonly referred to as **cytoplasm** and is limited externally by the **cell membrane**, which is also called

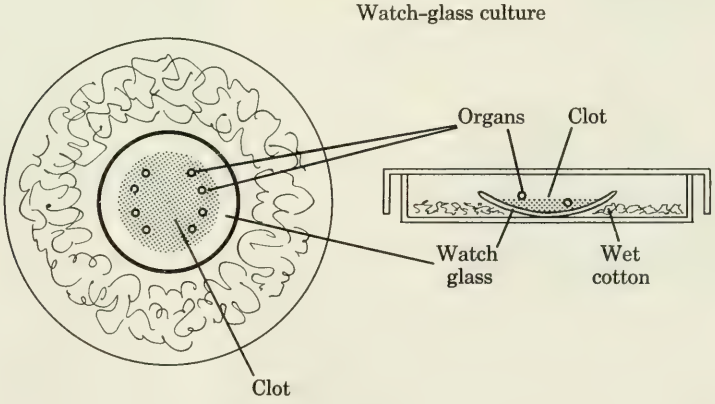


Fig. 2.5. An organ culture; diagrammatic.

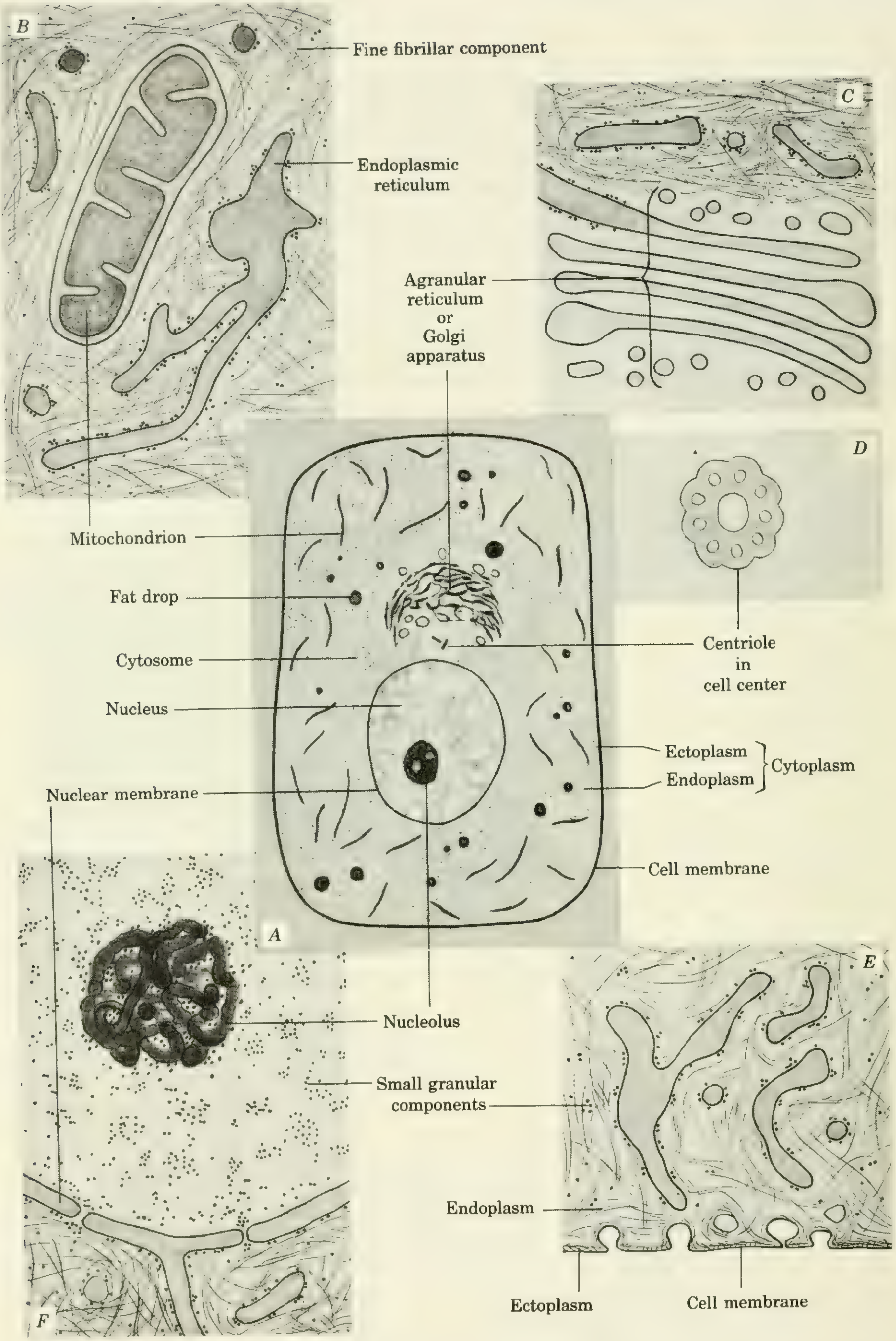

B
Fine fibrillar component
C
Endoplasmic reticulum
Agranular reticulum or Golgi apparatus
D
Mitochondrion
Fat drop
Centriole in cell center
Cytosome
Nucleus
Ectoplasm
Endoplasm
Cytoplasm
Nuclear membrane
Cell membrane
A
E
Nucleolus
Small granular components
Endoplasm
F
Ectoplasm
Cell membrane

Fig. 2.6. The structure of a composite animal cell as revealed by the light microscope (*A*) and the electron microscope (*B–F*); diagrammatic. The centriole in *D* is shown in cross section. (The authors are indebted to Keith R. Porter, George E. Palade, and Don W. Fawcett for discussions concerning this figure but accept full responsibility for any errors of interpretation in view of the recognized incompleteness of knowledge concerning the fine structure of cells.)

the **plasma membrane** (Fig. 2.6*A* and *E*). This is the semipermeable barrier through which everything entering or leaving the cell must pass. Elucidation of its structure has defied the highest magnification of the electron microscope. If photographs of isolated cells in tissue culture are taken at frequent intervals through a light microscope, a remarkable phenomenon called **pinocytosis** is revealed. This involves the "gulping," as it were, of fluid outside the cell through what are apparently small temporary breaks in the plasma membrane. In electron micrographs of sections of cells, minute vesicles are seen to be continuous through the plasma membrane with the intercellular space (Fig. 2.6*E*). These may indicate that pinocytosis occurs on a very small scale when cells are in their normal positions, but this is not an established fact. If the plasma membrane is grossly torn or otherwise damaged during manipulation, the contents of a cell escape and become disorganized; the cell dies. If the break is very limited, the plasma membrane may be reformed after minimal loss has taken place and the cell remains alive.

In cells that occur singly, such as the unicellular animals and the egg cells of some marine animals, there is a narrow zone of relatively firm or gel-like cytoplasm immediately internal to the plasma membrane (p. 230). This **ectoplasm** is relatively dense to electron penetration and contains many very fine fibers as seen in electron micrographs (Fig. 2.6*E*). An ectoplasmic zone is found at the exposed surfaces of cells lining many tubes, such as the digestive tract, in many-celled animals. However, ectoplasm cannot be distinguished at the periphery of cells that are in close association with one another. Instead, the cytosome is crowded with many different structures distributed in a relatively fluid ground substance or **endoplasm**, such as is found beneath the ectoplasm of free cells.

Under high magnification with the light microscope, the endoplasm appears to contain delicate fibers which many have thought formed a net or reticulum. In electron micrographs this **endoplasmic reticulum** is seen to be a system of canals, sharply limited by a continuous membrane (Fig. 2.6*B*). These channels are very narrow in places but widen in varying degree as they course throughout the endoplasm and communicate with the nuclear envelope in a manner to be described presently. The contents of the canals are of variable but low density and are unidentified chemically. With the magnification and resolution of the electron microscope, the endoplasm is found to contain great numbers of a **fine fibrillar component** (Fig. 2.6*B*). These seem to be like the very fine fibers present in the ectoplasm and are undoubtedly responsible for the viscosity of the cytoplasm.

Embedded in the endoplasm in the interstices of the reticulum are the rod-shaped **mitochondria**, found in varying numbers in all types of cells (Fig. 2.6*A*). In photographs of isolated cells in tissue cultures taken at frequent intervals through a light microscope, the mitochondria are seen to be in a constant state of flux—bending, fragmenting, uniting, and being carried from place to place by streaming of the endoplasm (Fig. 2.7*B*). The electron microscope reveals that each mitochondrion is bounded by a continuous envelope consisting of two

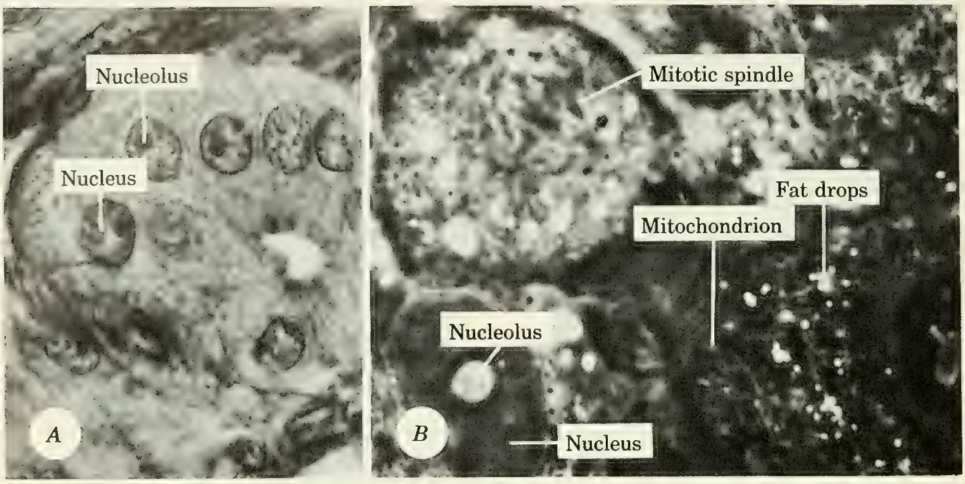


Fig. 2.7. Animal cells. *A*, section of fixed and stained cells as seen with the light microscope; ×1080. *B*, living cells of a tissue culture as seen with the phase microscope; ×1080. (*B*, courtesy George O. Gey.)

layers, the inner of which has characteristic folds extending into the matrix of the mitochondrion (Fig. 2.6*B*). Biochemical studies of mitochondria centrifuged out of cell homogenates have shown them to contain a number of enzymes necessary for oxidative metabolism in the cell (p. 36).

Specialized cells of one sort or another contain characteristic products of cellular metabolism. In gland cells there may be **secretion granules** of protein, as in the pancreas, or of fat, as in the mammary gland. **Fat drops** occur as storage material in many cells (Figs. 2.6*A* and 2.7*B*), and **yolk** is typically found in egg cells. **Glycogen** is a characteristic storage product in liver cells (p. 77); **pigment granules** occur in various kinds of cells.

A second structure of universal occurrence in the cytosome, identified only with the aid of the extreme magnification of the electron microscope, is called simply the **small granular component** (Fig. 2.6*E*). In any cells that are recognized as being highly differentiated in a metabolic sense, such as gland cells and nerve cells, most of the granules lie against the outside of the membranes bounding the cavities of the endoplasmic reticulum and on the outer nuclear membrane. In growing and dividing cells, on the other hand, the characteristic position of these dense granules is in the ground substance. Evidence from a number of sources indicates that these granules contain ribonucleic acid (RNA) and protein (pp. 27 and 28). Ribonucleic acid is responsible for the characteristic staining of certain kinds of cells, but more important is its role as a major factor in cellular synthesis of protein. When cells are homogenized and differentially centrifuged, one fraction contains so-called microsomes. Apparently these are fragments of the membrane of the endoplasmic reticulum together with the associated small granular components.

Another structure is almost universally found in the cytosome of the animal cell. It is the **cell center,** a small area appearing homogeneous when seen with the light microscope except for the presence of two small rods, the **centrioles;** these characteristically lie at right angles to one another (Fig. 2.6*A*). Electron micrographs reveal an amazing uniformity in the internal structure of these minute rods in all types of cells (Fig. 2.6*D*). The cell center is actively involved in the process of nuclear division and will be considered further in that connection (p. 39). In the region of the cytosome about the center in some but not all kinds of cells, it is possible to demonstrate with special histological techniques an irregular, coarse net-like structure known as the **Golgi apparatus** (Fig. 2.6*A*). Electron micrographs reveal in many cells a portion of the endoplasmic reticulum which lacks the small granular components typically found on its membrane. It is called the **agranular reticulum** and is associated with numerous vesicles; together, these are assumed to be the Golgi apparatus (Fig. 2.6*C*). Little is known of the biochemistry or function of this structure.

We come now to the **nucleus,** which is usually rounded and located somewhat centrally in the cell (Fig. 2.6*A*). The nucleus is surrounded by a distinct **nuclear membrane** or **envelope,** as seen in the light microscope. Electron micrographs reveal that the nuclear envelope actually consists of two closely associated layers, each of which is porous (Fig. 2.6*F*). Through the pores, which are common to both layers, the ground substance of the nucleus is continuous with the endoplasm. The space between the two layers of the nuclear envelope is continuous with the canals of the endoplasmic reticulum by way of pores in the outer layer.

Nuclei examined with the light microscope after fixation and staining appear to contain irregular, densely stained clumps of chromatin and one or more rounded **nucleoli** disposed on a delicate network (Fig. 2.7*A*). Nuclei of living cells examined with the phase-contrast microscope appear empty except for one or more nucleoli (Fig. 2.7*B*). Electron micrographs substantiate the inferences made from observations with phase-contrast lenses. The nucleus is seen to contain numerous small granules distributed without pattern (Fig. 2.6*F*); these are similar to the small granules of the cytosome. The nucleolus is a densely packed mass of granules, sometimes in linear order, not bounded by a membrane. Nucleoli are known to contain RNA and protein. As we shall learn when nuclear division is described under the discussion of cell division, very precisely arranged strands of chemical molecules, the genonemata, or gene strings, exist in the nucleus. Their dimensions are such that even the electron microscope cannot reveal them in the intervals between divisions of the cell. It has been determined, however, that genonemata are made up of desoxyribonucleic acid (DNA) which together with characteristic proteins forms the chromosomes seen in the nucleus of the dividing cell (pp. 39 and 40). The compounds of the genonemata are recognized as the directive agents of metabolism which confer uniqueness on both the individual and his species. Synthesis of precise replicas of these compounds is the means by which continuity of the orderly pattern of cellular events is insured within an individual as well as between generations.

Both nucleus and cytosome are necessary for the normal activities of the cell, but it is not yet known exactly what part each plays in the metabolism of the whole. Cells that are deprived of their nuclei are unable to carry on anabolism, although catabolism continues until the energy reserves are exhausted. The nucleus is the seat of nucleic acid synthesis, both DNA and RNA. The DNA located in the genonemata is sometimes referred to as a "set of instructions" for cellular function or as the "memory" of the cell, insuring orderly continuity of life processes. Continuing the interpretation in this vein, RNA, which passes from the nucleus to the endoplasm, functions as a "messenger," carrying instructions from nucleus to cytosome. In experiments with the unicellular amoeba (p. 230) from which the nucleus was removed, it was found that within 24 hours the RNA content was lowered, and cellular metabolism was defective. These amoebas continued to live for a number of days, and if a fresh nucleus was inserted within three days, normal conditions were restored. It cannot be doubted that there is very close interdependence between the two morphological divisions and that the life of the cell depends on integrated interaction between nucleus and cytosome.

The Chemical Nature of Protoplasm[1]

Although Thomas Huxley in his famous essay "On the Physical Basis of Life" (1868) discussed protoplasm as though it were a living chemical compound, and although the phraseology which uses "living matter" as synonymous with the contents of cells carries the same implication, it is now known that protoplasm is not a single compound. Rather, it is a highly complex system containing a great number of chemical compounds.

The most abundant single compound in the cell is water, which is, of course, a widely distributed inorganic compound. Present, too, are many familiar inorganic salts. The compounds that are unique for cells are known as organic compounds and are obtained naturally only from animals and plants. Characteristically, such compounds are combustible; that is, they break down into their constituent parts during burning, and all contain carbon. Most of them also contain hydrogen and a large number oxygen as well.

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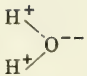
[1] Functions of living organisms cannot be explained without recourse to information which has been gained about the chemistry of cells. The basic chemistry of the cell will be explained in the simplest terms consistent with accuracy. Since the chemical backgrounds of students registered in an elementary course in zoology will usually vary greatly, it is assumed that some may have to consult elementary textbooks in chemistry or get help concerning specific points from their instructors.

In many, nitrogen is an added constituent and sulfur, phosphorus, or iodine may be present in some compounds. There are three great groups of the organic compounds present in relatively large amounts in cells. These are the carbohydrates, lipids, and proteins. Organic compounds which do not fall in these three groups are present in small amounts. These different categories of chemical compounds will be briefly described in this section in order that the nature of food and the changes which occur in it within the animal can be adequately discussed in the remainder of the chapter.

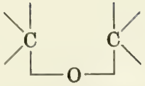
Water constitutes 60 to 90 per cent of the cell contents and holds the inorganic salts and many of the organic compounds in solution. The physical characteristics of water that are responsible for its great importance in the phenomena of life are shared by only a few other compounds—ammonia (NH_3), hydrogen peroxide (H_2O_2), and hydrogen fluoride (HF). With sufficient knowledge of chemistry and zoology we could speculate concerning hypothetical creatures with liquid ammonia as the solvent in their reacting systems. Instead, we shall attempt to grasp the essentials of animal life as it really exists.

Two atoms of hydrogen and one of oxygen are joined by covalent bonds, that is, by a sharing of electrons, to form a molecule of water. The two atoms of hydrogen are located on the same side of the oxygen atom, about 105° from one another (Fig. 2.8*A*). In other words, the water molecule is asymmetric or polarized, tending to behave as if positively charged on the hydrogen side and negatively charged on the oxygen side. This results in marked electrical attraction between the hydrogen side of one water molecule and the oxygen side of another. Such intermolecular electrostatic attraction between water molecules is known as hydrogen bonding and is responsible for the relatively high melting and boiling points of water as compared with other compounds of its chemical family. The importance of the relationship between the temperature range of the liquid state of water (0 to 100°C.) and that of the earth's surface is obvious. Hydrogen fluoride, another good solvent, melts at about -92°C. and boils at $+19$°C. Where living organisms can exist is basically conditioned by the melting and boiling points of water, the solvent of the cell contents. Other physical qualities of water make it exceptionally useful in the equalization of heat in organisms and in connection with temperature regulation in warm-blooded animals (p. 125).

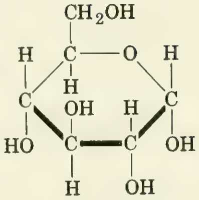
The **inorganic constituents** of the cell occur either as salts or in combination with certain of the organic molecules. When an acid and a base combine to form a salt, ions carrying opposite electrical charges are brought together and held by electrostatic attraction or what are known as ionic bonds. Salts are not soluble in most solvents, but the polarized molecules of water tend to neutralize the electrostatic attraction between the ions of a salt molecule. Once separated, the ions become encapsulated by water molecules and cannot recombine. Thus salts may be almost completely dissociated, or ionized, in the cell and body fluids and form an electrolytic solution that can conduct an electrical current. Sodium (Na^+), potassium (K^+), calcium (Ca^{++}),



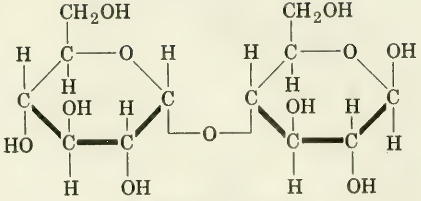
A. Water: H_2O



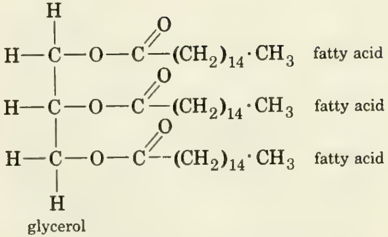
B. Glycosidic linkage



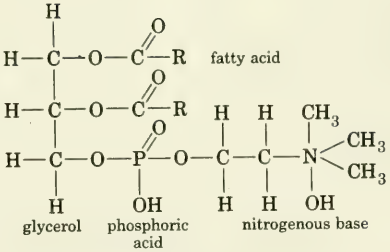
C. Glucose: $C_6H_{12}O_6$



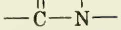
D. Maltose: $C_{12}H_{22}O_{11}$


fatty acid
fatty acid
fatty acid
glycerol

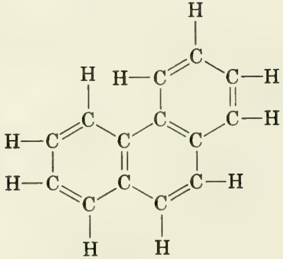
E. Palmitin: $C_3H_5 \cdot (C_{15}H_{31}COO)_3$


fatty acid
glycerol
phosphoric acid
nitrogenous base

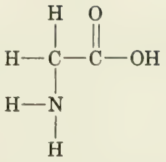
F. A lecithin



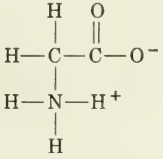
G. Peptide linkage



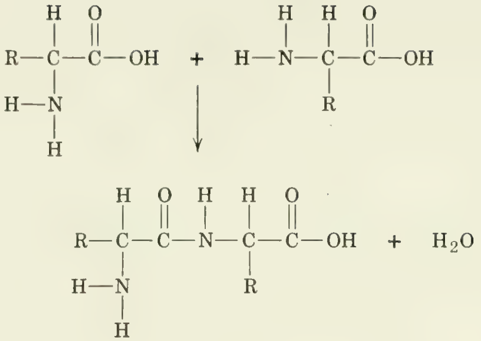
H. Phenanthrene: $C_{14}H_{10}$



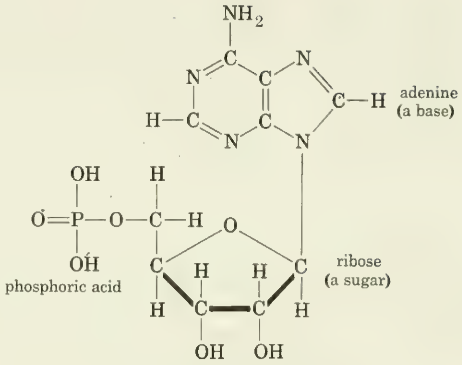
I. Glycine: $CH_2(NH_2)COOH$ (the simplest amino acid)



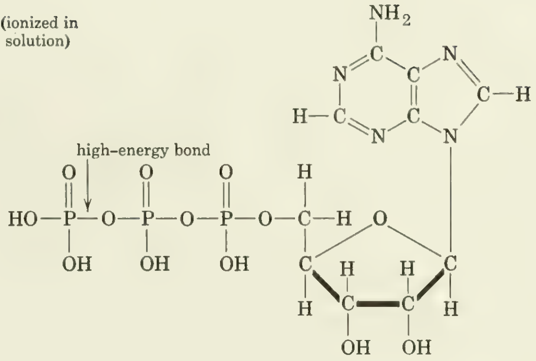
J. Glycine (ionized in aqueous solution)



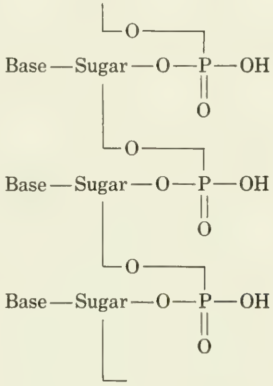
K. A dipeptide


adenine
(a base)
ribose
(a sugar)
phosphoric acid

L. Adenylic acid (a nucleotide)


high-energy bond

M. Adenosine triphosphate (ATP)



N. A polynucleotide

Fig. 2.8. Structural formulas of some chemical compounds related to cellular contents.

and magnesium (Mg^{++}) are indispensable cations in living systems, and phosphate ($HPO_4^{=}$), bicarbonate (HCO_3^{-}), chloride (Cl^{-}), and iodine (I^{-}) anions are also necessary for normal function. In addition, traces of iron (Fe^{+++}, Fe^{++}), cobalt (Co^{++}), and copper (Cu^{++}) cations, as well as of a few other metals, are found. Reference will be made to specific ions during the discussion of the functions of cells.

Carbohydrates are compounds containing carbon, hydrogen, and oxygen. Most of the carbohydrates can be classified as (1) monosaccharides, the simple sugars; (2) disaccharides, the compound sugars; and (3) polysaccharides, glycogen and the starches. Among the **simple sugars** are the five-carbon pentoses ($C_5H_{10}O_5$), which are rare, and the very common hexoses ($C_6H_{12}O_6$) such as glucose (Fig. 2.8*C*). The fact that the atoms of hydrogen and oxygen occur in the ratio of two to one in these sugars, as in water, is the reason for giving the name carbohydrate to the entire group. Two hexoses linked together form a **disaccharide** ($C_{12}H_{22}O_{11}$); maltose is formed by the linking of two molecules of glucose (Fig. 2.8*D*), and sucrose is a combination of one molecule of glucose and one of fructose. **Polysaccharides** are built up of many molecules of a single simple sugar joined, as in the formation of a disaccharide, by the so-called glycosidic linkage (Fig. 2.8*B*); glucose is usually the simple sugar involved. The sugars are soluble in water, but most polysaccharides are not. Carbohydrates are easily oxidized in the cell and are its chief source of the energy utilized for its work.

The **lipids** are a heterogeneous group of organic compounds containing chiefly carbon, hydrogen, and oxygen. These compounds are not soluble in water and are classified as (1) the simple lipids, including the fats and waxes; (2) the compound lipids; and (3) the steroids. **Simple lipids** are esters; an ester is a combination of an alcohol and an acid. Specifically, a chemically pure fat, such as palmitin, olein, and stearin, is an ester of glycerol and three molecules of a single fatty acid (Fig. 2.8*E*). Natural fats, such as butter, lard, and tallow, are mixtures of chemically pure fats. In the cell, fats are readily oxidized, with the liberation of energy, much of which is transformed into heat. Waxes, which are also simple lipids, commonly occur as secretions of insects and mammals; some oils, such as that of the sperm whale, contain waxes. They are esters of alcohols other than glycerol, together with free alcohols and fatty acids. Among the **compound lipids**, the phospholipids, such as lecithin which is common in egg yolk, contain phosphoric acid and a nitrogenous base, such as choline, in addition to glycerol and fatty acids (Fig. 2.8*F*). Another group of compound lipids known as the cerebrosides, because they are commonly found in nervous tissue, are combinations of a fatty acid, a nitrogen-containing alcohol, and a simple sugar. **Steroids** are crystalline, alcoholic compounds characterized by the presence of the complex phenanthrene ring system (Fig. 2.8*H*). This group contains cholesterol which is of widespread occurrence, vitamin D, the sex hormones, and the hormones of the adrenal cortex, all of great physiological importance.

Proteins are the most abundant group of organic compounds in the cell. All simple proteins contain carbon, hydrogen, oxygen, and nitrogen; in some, sulfur and iodine occur. Proteins may be conjugated with carbohydrates to form glycoproteins, with lipids to form lipoproteins, with nucleic acids (see below) to form nucleoproteins, with metal ions (Fe^{++}, Fe^{+++}, Cu^{++}, Zn^{++}, Mn^{++}) to form metalloproteins. Proteins are very large molecules with representative molecular weights as follows: insulin, a hormone, 12,000; pepsin, a digestive enzyme, 34,500; egg albumin, 40,000; hemoglobin, a respiratory pigment, 68,000; and myosin, a contractile fiber, 850,000. There are at least 25 different amino acids (Fig. 2.8*I*), which are combined in varying proportions and sequences to form the uncounted kinds of protein molecules. In the formation of a simple protein, the different kinds of constituent amino acids ($R{\cdot}CH{\cdot}NH_2{\cdot}COOH$) are linked together by bonding between the nitrogen atom of the amine group (NH_2) and the carbon atom in the carboxyl group (COOH); this is known as the peptide linkage (Fig. 2.8*G*). Two amino acids so linked are called a dipeptide (Fig. 2.8*K*); longer chains are tri- and polypeptides. These chains are loosely coiled, and adjacent strands are held together by hydrogen bonds to make a very complex chemical structure. Chemists have, however, succeeded in determining the exact kinds and sequences of the amino acids present in a few proteins; the pancreatic hormone insulin is an example.

It should be noted that amino acids contain both a basic (NH_2) and an acidic (COOH) group. In aqueous solution, these groups ionize, and the amino acid becomes an electrically polarized molecule, carrying both a positive and a negative charge (Fig. 2.8*J*). Although the peptide linkages in a polypeptide chain involve most of the ionizable groups, the terminal NH_2 and COOH groups ionize when a protein is in solution, as many are within the cell. Depending on the acidity of the solvent, proteins may carry both a positive and a negative charge and behave as though electrically neutral. On the other hand, they may be partially dissociated and behave either as positive ions or as negative ones.

The proteins of the cell, together with certain lipids, play a major role in maintaining the morphological features of cells, such as membranes. Different kinds of animals are characterized by specific proteins which endow them with their unique qualities. Proteins are extremely sensitive to changes in their surroundings such as heat and degree of acidity. They may undergo modification, involving the breaking of the hydrogen bonds of the molecule, which results in loss of capacity to take part in cellular reactions.

Nucleic acids are a group of complex organic compounds present in small amounts in the cell. The structural unit of the nucleic acids is the nucleotide, of which only nine different ones have been isolated from the nucleic acids. These nucleotides are composed of a nitrogenous base, a pentose sugar, and phosphoric acid (Fig. 2.8*L*); they are linked (Fig. 2.8*N*) in varying sequence to form the very large molecules of nucleic acid. Depending on the kind of pentose sugar present in the molecule, there are two classes of nucleic acid. One contains desoxyribose and is known as desoxyribonucleic acid (DNA); it is localized in the nucleus and is of major importance in inheritance (p. 197). The other contains ribose and is called ribonucleic acid (RNA); this type is basically concerned in the synthesis of proteins, perhaps determining their pattern and thus their quality of specificity. In addition to the function of RNA in protein synthesis, nucleic acids may be conjugated with proteins to form the nucleoproteins; nucleic acid forms the core of the enormous spiraled molecule. It is known that some nucleoproteins, such as those of the chromosomes which contain DNA (p. 39), and virus particles which contain RNA, are capable of self-duplication; indeed, viruses are often considered to be living organisms. In the chromosome and virus it is the nucleic acid moiety which endows the whole with its unique functional quality.

Enzymes are proteins which act as organic catalysts. A catalyst is a substance, whether inorganic or organic, that accelerates a chemical reaction without affecting the character of its end products. An enzymatic protein frequently has to have another compound known as a coenzyme combined with it before it becomes effective as a catalyst; some metalloproteins function as enzymes. Enzymes are effective in very small amounts and are unchanged by the reactions in which they participate. The substance that is acted upon by an enzyme is known as its substrate. Enzymes catalyze reactions, reactions that would otherwise proceed very slowly, by becoming associated or combined with some particular region of the substrate molecules. The enzyme is an asymmetrical molecule of such a shape that ordinarily it alone can occupy a particular niche in the substrate molecule. A compound with molecules that are quite similar to those of a particular enzyme can sometimes be used to inhibit or block a reaction normally catalyzed by that enzyme; the inhibitor molecules pre-empt the substrate niches in which the enzyme must be present if the reaction is to occur. The association of enzyme with substrate apparently facilitates the transfer of electrons involved in the reaction. When the substrate molecule is changed, either broken apart or combined with another molecule, the enzyme is no longer associated. It is free to combine with another substrate molecule and catalyze its reaction. Within the cell, the end products of one enzyme-catalyzed reaction rarely accumulate; instead, they are immediately involved in other enzyme-catalyzed reactions. Expenditure of energy is required to drive certain chemical reactions, and in others energy is released. The end products of many enzyme-catalyzed reactions which release energy are involved in reactions which require energy. Such coupled reactions make possible the continuous sequences which characterize the metabolism of cells.

Enzymes exhibit extreme specificity with respect to their substrates. It is obvious that with the multiplicity of chemical compounds occurring in cells there must be a great many enzymes. Enzymes may be thought of as machines carrying out specialized operations in a factory. Each is a part of an integrated enzyme complex that is coming to be recognized as the essence of the living state in the cell. The enzymes of the cell maintain the steady state of utilization of food, transfer of energy, and synthesis of cellular components. They control the pace and the pattern of cellular life.

Food

Food is necessary for the maintenance of the structure and function of cells; it provides the chemical units needed to replace the ones that are constantly being destroyed in metabolic processes and lost by excretion (p. 82). In young organisms growth depends on proper food; and food is the fuel that provides the energy required to do the mechanical, electrical, and chemical work of the organism. If the chemical nature of the cell contents is recalled, it will be evident that food must contain water, inorganic salts, carbohydrates, lipids, and proteins. In addition, a group of compounds known as vitamins is necessary.

Water, which is the most abundant constituent of the cell and body, is also, with the exception of oxygen, the most important. It is present as such in the so-called solid foods which are consumed and is produced in the cell by the oxidation of organic foods. Water is taken in as such by terrestrial vertebrates, and man supplements his intake with a variety of beverages.

Although **inorganic salts** constitute only a small percentage of the chemical compounds of the organism, they are of widespread importance. Inorganic ions are components of various enzyme systems, of several vitamins and hormones, and of respiratory pigments; they are required for such processes as the conduction of nerve impulses, the contraction of muscle, and the clotting of blood. The diet must contain calcium, phosphorus, sodium, potassium, magnesium, sulfur, and chlorine, which together comprise 60 to 80 per cent of the total inorganic material of the human body. In addition, traces of iron, copper, iodine, manganese, cobalt, and zinc are required. Milk is a source of calcium and phosphorus, both of which are necessary in proper proportion for formation and maintenance of bone. Phosphorus is also exceedingly important in cellular metabolism, as we shall see. Other inorganic substances are obtained from milk, from drinking water, and from plants grown on soils containing adequate amounts of minerals.

To determine the energy value of various food constituents, the chemist burns or oxidizes them in a bomb calorimeter; the amount of heat given off in this complete combustion is measured in calories. A calorie is the quantity of heat required to raise the temperature of one gram of water one degree centigrade. Some of the energy which is released from food during cellular metabolism (p. 37) is transformed into heat which affects the body temperature. Special heat-regulatory mechanisms in warm-blooded animals, the birds and mammals, control loss of heat and make possible a relatively constant body temperature (p. 125).

The hexose **carbohydrates** are the most efficient source of energy available in the diet. Glucose in excess of the immediate requirements of cellular metabolism can be built up into the polysaccharide glycogen and stored for future use. Some of the polysaccharides, such as the cellulose occurring in plants, cannot be digested by man and comprise part of the roughage which gives necessary bulk to the feces.

Lipids in the diet provide a major source of energy for the animal. When oxidized, fats yield over twice as much energy per unit weight as other foods. Also, the oxidation of fat releases about twice as much water as other foodstuffs. This is an important factor in providing some animals with a supply of water under adverse conditions. For example, the desert-dwelling camel stores much fat and has a high level of fat metabolism. Also, the developing chick embryo, shut off for 21 days from supplies outside its eggshell, gets its necessary water from the oxidation of the lipid which makes up about 90 per cent of the dry weight of the yolk of the hen's egg. About 1 per cent of the dietary lipid must contain what are called essential fatty acids, of which there are three. These are unsaturated fatty acids found in many food oils. In their absence, various skin and nervous disorders may occur in man; the cellular basis for these disturbances is not known. Both carbohydrates and proteins can be converted to fat in cellular metabolism, and such excess or reserve food is stored in cells as fat.

Proteins are an indispensable part of the diet for young and old. Growth and restoration of body proteins lost in daily activities can be accomplished only when a supply of amino acids is available. Of the 25 amino acids known to be constituents of proteins, only 8 are essential for human nutrition. This means that they must be supplied to man in his dietary protein because he is unable to synthesize them from other foodstuffs at a rate necessary for normal function. It is important that all the essential amino acids be provided in the required amounts at approximately the same time. If all the amino acids required for the synthesis of a particular protein are not simultaneously present, those that are present will be degraded and lost from the so-called protein pool. Amino acids, whether essential or non-essential, cannot be stored in cells. Protein foods are not equally efficient in supplying essential amino acids; eggs, dairy products, liver, and kidney contain all of them.

Vitamins are accessory dietary components which play important roles in cellular metabolism, although required in very small amounts. Members of this heterogeneous group of organic compounds are not sources of energy, nor are they used to replace worn-out cellular components. Instead, they make possible the utilization of other foodstuffs in normal metabolic sequences; some have been demonstrated to be coenzymes. Thus, inadequate amounts of vitamins may result in metabolic defects which in time give rise to clinically recognizable diseases.

To be classified as a vitamin for a particular kind of animal, the substance must be one which the animal requires in its food. This definition differentiates vitamins from hormones and enzymes, which also act in very small quantities but are produced in the body. When a certain compound is stated to be a vitamin, it is not to be inferred that all animals require it in their food. Certain animals can synthesize a compound which is a specific requirement for maintenance or growth, for example, or they may have bacteria living in their digestive tracts which can synthesize it. Other kinds of animals must obtain this same substance ready-made in the food they eat; for them, it is a vitamin. Vitamins are detected in studies of the specific nutritive requirements of different species of animals; rats are widely used in such laboratory studies. When these nutritional substances were first discovered, they were classified on the basis of their solubility in fats or in water. Letters were used for identification since their chemical structure was unknown. At present, the chemical formulas of all the commonly known vitamins have been determined. They may be designated now by names which either describe the compound chemically or indicate its source or major function.

The **fat-soluble vitamins** include those designated as A, D, E, and K. In each, two or more closely related chemical compounds have been found to give the effect originally assigned to a single vitamin. Deficiencies of the fat-soluble vitamins may result either from an inadequate diet or from a disturbance of the mechanism for fat absorption from the intestine.

Vitamin A is found only in the animal kingdom. It may be obtained, preformed, from milk, butter, egg yolk, and fish-liver oils. A precursor, or provitamin, called beta-carotene, is present in green and yellow vegetables. This compound can be converted to vitamin A by the animal. The physiological activity of vitamin A is concerned with the maintenance of the epithelia of exposed surfaces, such as epidermis of the skin and cornea of the eye. It also participates in the synthesis of visual pigments such as rhodopsin, or visual purple, a pigment of the retina of the eye necessary for vision, especially in dim light (p. 107). Deficiency of vitamin A results in excessive keratinization of the skin and cornea so that they become dry and horny, and in varying degrees of night blindness.

Vitamin D is a group name for at least ten different steroids, of which two, D_2 and D_3, are especially important to man in the development of teeth and bone. These vitamins increase the intestinal absorption of calcium and phosphorus and are required for the actual deposition of these substances in bone. Sources of this vitamin are fish-liver oils, butter, liver, and egg yolk. The content of vitamin D in milk can be increased by exposure to ultraviolet radiation which brings about the transformation of a precursor. The same kind of reaction occurs in human skin when it is exposed to sunlight. A deficiency of vitamin D results in rickets in children and in a similar disorder in adults, especially older ones. In each age group the bone is inadequately calcified, and deformities may result.

Vitamin E, another group of compounds, is known as the antisterility vitamin and is necessary for normal reproductive functions in the rat. The male becomes sterile in the absence of vitamin E; the female is unable to maintain the placentas for the nourishment of the embryos, and they are aborted. An entirely different result of deficiency of E vitamins in young rats and in rabbits and guinea pigs is degeneration of skeletal muscle, or muscular dystrophy. The E vitamins are chemically known as tocopherols and are available in green leafy vegetables, whole wheat, and egg yolk. Up to the present time, a requirement for tocopherols in human nutrition has not been established.

Vitamin K, the antihemorrhagic vitamin, is involved in an unknown way in the production of prothrombin in the liver and is, therefore, necessary for the normal clotting of blood (p. 64). A dietary deficiency of this vitamin, which is a naphtho-quinone, is unlikely since it has wide distribution in foods. Good sources are green leafy vegetables, tomatoes, cheese, egg yolk, and liver. In addition, bacteria normally present in man's digestive tract synthesize vitamin K, which is then absorbed. Certain sulfa drugs and other intestinal antiseptics may cause a deficiency by reducing the number of bacteria which produce the vitamin. Also, if absorption is interfered with, deficiency may result. In the absence of vitamin K, the amount of prothrombin in the blood is reduced and clotting time is prolonged. A deficiency of vitamin K occurs in newborn infants, since the intestine is sterile and the amount of the vitamin supplied by the mother is small. Sometimes bleeding may be severe, or even fatal. Some physicians routinely give supplementary vitamin K to expectant mothers in order to prevent hemorrhagic episodes in the newborn.

The first **water-soluble vitamin** to be identified was named vitamin B. It was soon realized that the effects attributed to vitamin B were related to a number of different substances, all of which were in some way growth-promoting. In other words, there was not a single B vitamin but, instead, what is referred to as the B complex. We shall consider some of the better-understood compounds in the complex, all of which are available in crystalline form.

Thiamine, or vitamin B_1, was the first member of the B complex to be identified. After its isolation from rice polishings, it was synthesized in 1936. Thiamine is fairly widely distributed in foods, especially in whole grains, legumes, lean meat, and yeast; however, only small amounts are present in any source. Thiamine deficiency is generally characterized by loss of appetite and consequent malnutrition. Later, neurological symptoms and dysfunction of the heart and other organs occur. It has been clearly shown that thiamine pyrophosphate is involved in the cellular metabolism of carbohydrate, functioning as a coenzyme called cocarboxylase (p. 36).

Riboflavin, lactoflavin, vitamin B_2 or G, is necessary for the growth of many animals, including man, and for the preservation of health in the adult. This vitamin occurs in yeast, milk, eggs, liver, and some vegetables. Riboflavin deficiency in man is widespread and gives rise to soreness at the angles of the mouth, inflammation of the tongue, and tissue damage in several parts of the eye. The physiological role of riboflavin is correlated with its union with phosphate to form flavin nucleotides which then combine with proteins. These complex flavoprotein molecules have multiple functions in oxidative metabolism as assistants to a number of enzymes (p. 37).

Nicotinic acid, niacin, or the antipellagric vitamin, protects man against the disease called pellagra, which was formerly very common in the Southern states and found throughout the nation. Pellagra is characterized by skin lesions, digestive disturbances, muscular weakness, and progressive impairment of the nervous system, often ending in insanity. In 1914 it was proved a dietary-deficiency disease. It has since been shown that pellagra probably results from scarcity of several of the B-complex vitamins, including thiamine and riboflavin. Education regarding proper diet and the medicinal use of nicotinic acid have reduced the incidence of the disease. Other animals exhibit pellagra-like symptoms; in dogs, the condition is called blacktongue. Niacin is abundant in fresh meat, liver, yeast, milk, eggs, and fish. This vitamin also functions in cellular oxidations, forming two coenzymes: coenzyme I, or diphosphopyridine nucleotide (DPN), and coenzyme II, or triphosphopyridine nucleotide (TPN). These are involved in several different steps in carbohydrate metabolism (p. 36), and DPN is essential for vision (see Fig. 4.16, p. 108).

Pyridoxine, vitamin B_6, was first found to be a dietary requirement for rats in which it prevented dermatitis. It was later shown to be essential for man, also, even though a deficiency disease for this vitamin has not been identified. Yeast, whole grains, egg yolk, milk, and liver are good food sources for pyridoxine. It plays an important role in various enzymatic reactions in amino acid metabolism in the cell.

Pantothenic acid is so widely distributed in food that, even on a restricted diet, man apparently gets enough; a deficiency syndrome is not known. In rats, mice, and chickens, however, deficiency leads to dermatitis and widespread disorder in other tissues, suggesting a basic function in cellular metabolism. Pantothenic acid contributes to the formation of an exceedingly important compound known as coenzyme A. This coenzyme takes part in the metabolism of carbohydrates, lipids including steroids, and proteins (p. 36).

Biotin, or vitamin H, is necessary for the growth of various birds but is not a dietary requirement for mammals, in which it is supplied by the intestinal bacteria. The feeding of raw egg white to mammals produces a biotin deficiency because the egg white combines with the biotin and renders it ineffective as a vitamin. Diarrhea, dermatitis, and nervous disorders are symptoms of biotin deficiency.

A group of vitamins of the B complex is designated the **folic acid** group; all are related to pteroyl glutamic acid. Folic acid is essential for growth in higher animals. Fresh green leafy vegetables, kidney, and liver are rich food sources. Intestinal bacteria also contribute to the supply of folic acid. Consequently, administration of certain sulfa drugs which act directly on the intestinal flora may contribute to a deficiency. Anemia is the most obvious defect in animals with a folic acid deficiency.

Knowledge of these growth substances has contributed to an understanding of the mechanism of action of a group of drugs, the sulfonamides, in combating bacterial infection. The various sulfonamides resemble para-aminobenzoic acid (PABA) which is a requirement for the synthesis of folic acid by some of the pathogenic bacteria. When the sulfa drugs are present, they block the utilization of PABA by the bacteria; folic acid is not synthesized, and the bacteria cease to grow. Since animal cells do not use PABA, they are not damaged by the drug.

Vitamin B_{12} is a unique type of chemical compound, characterized by its complex ring structure and containing one cobalt atom and a single cyanide group; it is known as cyanocobalamin. It was isolated in 1948, subsequently synthesized, and its molecular structure reported in 1955. Vitamin B_{12} is found chiefly in foods of animal origin, where it is present in very low concentration. Intestinal microorganisms synthesize B_{12}, which can then be absorbed. It has several functions, some in conjunction with folic acid, and participates in a variety of fundamental metabolic reactions. It also has a specific effect on the formation of blood cells and is often called the antipernicious anemia vitamin. Injections of B_{12} in patients with pernicious anemia usually produce dramatic relief of the anemia, as well as of the neurological symptoms of the disease. In addition, vitamin B_{12} is essential for the growth of young mammals.

Another type of water-soluble vitamin is **ascorbic acid**, vitamin C, or the antiscorbutic vitamin. It appears to be a dietary requirement for only a few animals, but man is one of them. Deficiency of ascorbic acid results in scurvy, characterized by bleeding through capillary walls. The cellular function of ascorbic acid remains unknown, except that it participates in some way in the formation of intercellular material. Citrus fruits and tomatoes are rich sources of this vitamin, and it is abundant in paprika and in the cortex of the adrenal gland.

In the light of modern investigations on the nutritional requirements of animals, it becomes evident that in order to secure a proper balancing of the diet we must do more than obtain a certain ratio between amounts of carbohydrates, lipids, and proteins. It is essential that the proteins contain the amino acids needed by the cells, that the inorganic constituents be present in proper concentrations, and that vitamins be furnished. Abnormal functions of the body conditioned by food inadequate in vitamins and minerals are serious factors in human welfare. On the whole, however, the very numerous cases of borderline malnutrition, predisposing the individual to various diseased conditions and allowing him to maintain only a low level of physical and mental efficiency, are of more importance to society as a whole. Every individual should eat abundantly of the protective foods containing vitamins.

It is characteristic of the nutrition of animals, with only a few exceptions (p. 242), that they cannot build their foods from the constituent chemical elements but must make use of compounds produced by the cells of other animals or of plants. The products of metabolism of one kind of organism are not ordinarily usable, as such, by another type of organism. Therefore, food, in addition to possessing the necessary qualities which have been discussed, must be utilizable by the animal eating it. The chemical processes of digestion which render food usable in cellular metabolism will be discussed in the following chapter.

Cellular Metabolism

Food is the fuel of the cell; the energy stored in its chemical bonds must be released by chemical reactions in order that the work of the cell can be done. The release of energy during cellular metabolism does not occur as the result of a vigorous reaction of burning, as in a calorimeter, during which the energy is dissipated as heat. Instead, the release of free chemical energy during metabolism occurs by the gentle degradation of organic molecules in an orderly and conservative manner. The handling of food molecules in this way is a very complex process. Long chains of reactions, each catalyzed by a different enzyme, are necessary to break down, bit by bit, the organic compounds of food. We shall consider, in as simplified a way as possible, some of the essentials of dynamic cellular chemistry in order that you may gain a better understanding of the metabolic processes common to all living cells. Some of you will not have sufficient knowledge of chemistry to appreciate all the implications of the following account. You should, however, be able to follow the main line of the presentation and gain some conception of the intricate precision which characterizes life at the cellular level. If the material is too difficult for you, your teacher may suggest that you omit this section.

It is necessary to recall that in some chemical reactions energy is liberated when a bond is broken and in others energy must be used to break a bond. There are a few compounds that carry unusually large amounts of energy in certain of their bonds; the breaking of such high-energy bonds releases free energy which can then be used to drive reactions requiring that work be done. This relationship implies that the compound carrying or storing energy must constantly be replaced in order that the chemical sequences of cellular metabolism can continue. There is one exceedingly reactive compound that supplies the great amounts of free chemical energy required to do the work of the cell. This is adenosine triphosphate, known as ATP (Fig. 2.8*M*); when its terminal (third) phosphate bond is broken, nearly 12,000 calories of free energy become available for use, per mole of ATP. Such a bond is known as a high-energy phosphate bond.

Carbohydrate has already been identified as the chief source of fuel for the cell. However, carbohydrates do not react directly with oxygen in the cell, nor do they immediately break down into carbon dioxide and water. The production of these two waste products of cellular metabolism occurs in the final phase of the metabolism not only of carbohydrate but of lipid and protein, as well. Either glycogen, the stored polysaccharide carbohydrate made up of many glucose molecules, or glucose itself can be used by the cell. The steps in carbohydrate metabolism are subdivided into two groups, dependent upon the absence or presence of oxygen; these are the anaerobic (without oxygen) phase and the aerobic (with oxygen) phase.

Considering first the anaerobic phase, most of the reactions involve addition, subtraction, or rearrangement of phosphate groups in the molecule (Fig. 2.9). The first step in carbohydrate metabolism is the addition of a phosphate group to glucose. This reaction is called a phosphorylation and is catalyzed by a specific enzyme. In the course of the reaction, ATP donates its terminal phosphate group to the glucose, so that the resulting hexosephosphate is a high-energy compound. Similarly, another phosphate group from another ATP molecule is added to form a hexose diphosphate. This six-carbon compound is then split, under the influence of another specific enzyme, to yield two molecules of a three-carbon compound designated as a triose. Each of these contains one high-energy phosphate bond and next obtains a low-energy phosphate group from the inorganic store. Under the influence of a different enzyme, two hydrogen atoms are removed from the triose diphosphate. This reaction is known as a dehydrogenation and occurs only when coenzyme I, or DPN (p. 33), is present to accept, or combine with, the released hydrogen atoms. As a result of changes occurring in the molecule during the dehydrogenation, it now contains two high-energy phosphate bonds. In a series of reactions the three-carbon compound is converted to pyruvic acid which is the typical end product of anaerobic carbohydrate metabolism. However, some cells are capable of modifying pyruvic acid under anaerobic conditions. For example, muscle cells form lactic acid from it, and yeast cells convert it to alcohol.

During the conversion of each molecule of glucose to two molecules of pyruvic acid, some free energy is harnessed by means of coupled reactions (p. 28). Thus, four molecules of ATP are formed during the series of steps which make use of energy from two molecules of ATP to run the reactions; the cell has made a net gain of two ATP molecules. If glycogen, stored in the cell, is the starting material, only one molecule of ATP is required to drive the anaerobic phase so that the net energy gain is represented by three molecules of ATP.

During the aerobic phase of carbohydrate metabolism, pyruvic acid is broken down into carbon dioxide and water, and the bulk of the energy originally stored in the hexose molecule is released in small packets. The first step involves removal of one molecule of carbon dioxide from the pyruvic acid to form acetic acid, a two-carbon compound; this enzymatic reaction requires the coenzyme cocarboxylase (p. 32). Next acetic acid enters into combination with coenzyme A (p. 33), in the presence of ATP, to form acetyl coenzyme A. Only then does the carbohydrate food material enter the series of reactions known as the tricarboxylic acid (TCA) cycle which is the pathway for oxidation of not only carbohydrates but lipids and proteins, as well.

The reactions of the TCA cycle involve formation of citric acid, a six-carbon acid, from acetyl coenzyme A and a four-carbon acid, oxaloacetic

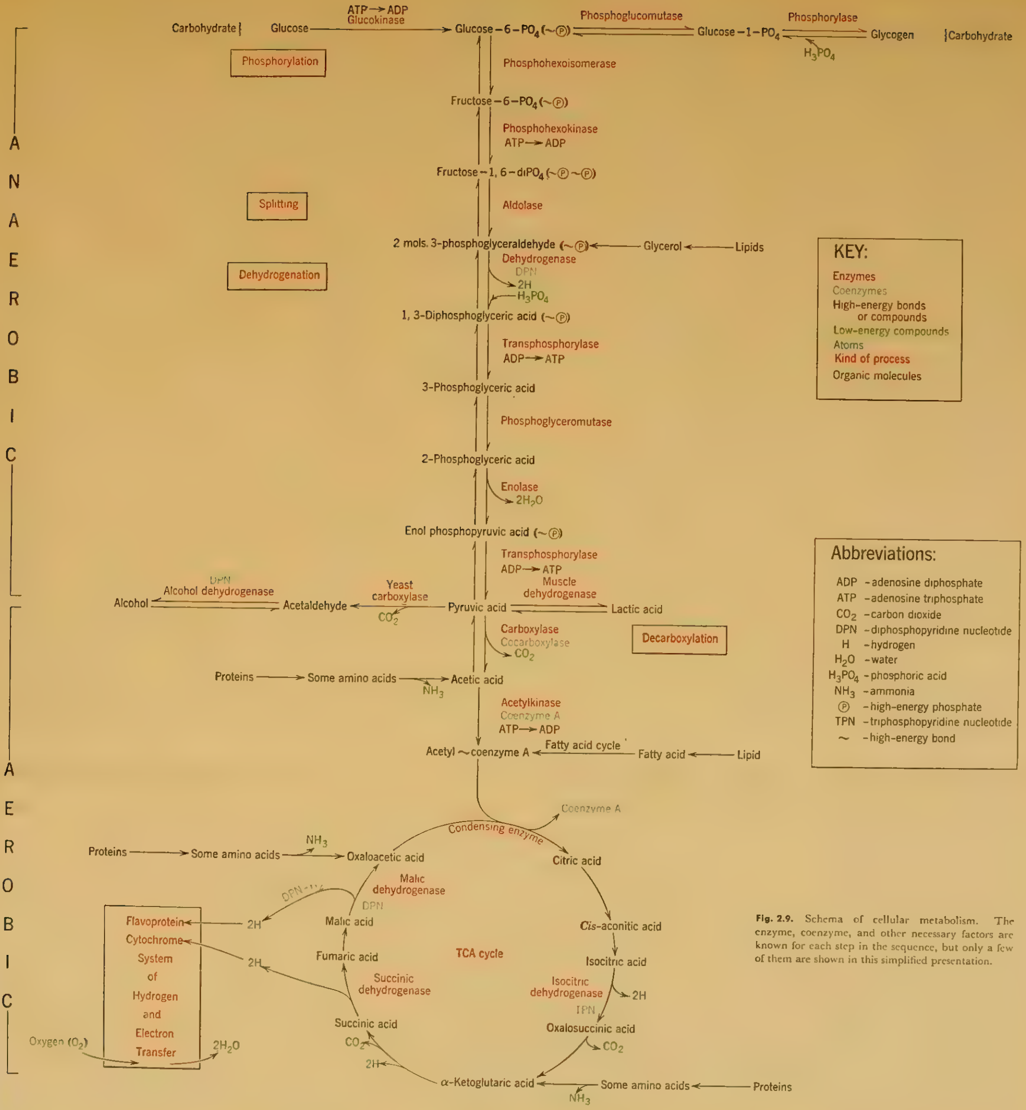

ANAEROBIC
AEROBIC
Carbohydrate
Glucose
ATP → ADP
Glucokinase
Glucose − 6 − PO_4 (~Ⓟ)
Phosphoglucomutase
Glucose − 1 − PO_4
Phosphorylase
Glycogen
H_3PO_4
Carbohydrate
Phosphorylation
Phosphohexoisomerase
Fructose − 6 − PO_4 (~Ⓟ)
Phosphohexokinase
ATP → ADP
Fructose − 1, 6 − diPO_4 (~Ⓟ ~Ⓟ)
Splitting
Aldolase
2 mols. 3-phosphoglyceraldehyde (~Ⓟ)
Glycerol
Lipids
Dehydrogenation
Dehydrogenase
DPN
2H
H_3PO_4
1, 3-Diphosphoglyceric acid (~Ⓟ)
Transphosphorylase
ADP → ATP
3-Phosphoglyceric acid
Phosphoglyceromutase
2-Phosphoglyceric acid
Enolase
$2H_2O$
Enol phosphopyruvic acid (~Ⓟ)
Transphosphorylase
ADP → ATP
DPN
Alcohol dehydrogenase
Alcohol
Acetaldehyde
Yeast carboxylase
CO_2
Pyruvic acid
Muscle dehydrogenase
Lactic acid
Carboxylase
Cocarboxylase
CO_2
Decarboxylation
Proteins
Some amino acids
NH_3
Acetic acid
Acetylkinase
Coenzyme A
ATP → ADP
Acetyl ~ coenzyme A
Fatty acid cycle
Fatty acid
Lipid
Coenzyme A
Condensing enzyme
Proteins
Some amino acids
NH_3
Oxaloacetic acid
Citric acid
Malic dehydrogenase
DPN
DPN
2H
Malic acid
Cis-aconitic acid
Flavoprotein
Cytochrome
System of Hydrogen and Electron Transfer
2H
Fumaric acid
TCA cycle
Isocitric acid
Succinic dehydrogenase
Isocitric dehydrogenase
2H
TPN
Succinic acid
Oxalosuccinic acid
Oxygen (O_2)
$2H_2O$
CO_2
CO_2
2H
α-Ketoglutaric acid
Some amino acids
Proteins
NH_3
KEY:
Enzymes
Coenzymes
High-energy bonds or compounds
Low-energy compounds
Atoms
Kind of process
Organic molecules
Abbreviations:
ADP − adenosine diphosphate
ATP − adenosine triphosphate
CO_2 − carbon dioxide
DPN − diphosphopyridine nucleotide
H − hydrogen
H_2O − water
H_3PO_4 − phosphoric acid
NH_3 − ammonia
Ⓟ − high-energy phosphate
TPN − triphosphopyridine nucleotide
~ − high-energy bond

Fig. 2.9. Schema of cellular metabolism. The enzyme, coenzyme, and other necessary factors are known for each step in the sequence, but only a few of them are shown in this simplified presentation.

acid. This four-carbon acid is an essential component of the TCA cycle and must be reformed to prime the system for the oxidation of a second two-carbon molecule. In the series of reactions occurring during each turn of the TCA cycle, two more molecules of carbon dioxide are split off. Such reactions are called decarboxylations and are coupled with dehydrogenations. The hydrogen atoms removed in these reactions become associated with what are known as carrier compounds which relay them through the flavoprotein (p. 32) and cytochrome transfer system to a final reaction with oxygen to form water. These reactions are referred to as biological oxidation, or cellular respiration, because in order to proceed they require oxygen. During the reactions leading to complete oxidation of one two-carbon compound in the TCA cycle, free energy is stored in at least 16 molecules of ATP.

A better appreciation of the efficiency of the cellular mechanisms for the release and subsequent storage of energy can be gained by consideration of the following balance sheet for carbohydrate metabolism. Combustion of glucose in a bomb calorimeter produces the end products carbon dioxide and water and releases energy in the form of heat:

$$\begin{aligned}&1 \text{ glucose } (C_6H_{12}O_6) + 6 \text{ oxygen } (O_2) \longrightarrow 6 \text{ carbon dioxide } (CO_2)\\&\qquad + 6 \text{ water } (H_2O) + 673{,}000 \text{ calories of energy (heat)}\end{aligned}$$

In the cell, as a result of anaerobic sequences:

$$1 \text{ glucose } \xrightarrow[\text{ATP}]{\text{Enzymes}} 2 \text{ pyruvic acid} + 58{,}000 \text{ calories of free energy,}$$

of which 48,000 calories are stored in four gram molecules of ATP. The aerobic reactions, on the other hand, release a far greater amount of energy:

$$\begin{aligned}&2 \text{ pyruvic acid} + 10 \text{ oxygen } (O_2) \xrightarrow[\text{ATP}]{\text{Enzymes}} 6 \text{ carbon dioxide } (CO_2)\\&\qquad + 4 \text{ water } (H_2O) + 420{,}000 \text{ calories of free energy,}\end{aligned}$$

of which 384,000 calories are stored in 32 gram molecules of ATP.

During the metabolism of a mole of glucose, approximately 480,000 calories of its total of 673,000 calories of energy are stored in ATP and thus made available for the work of the cell. The operating efficiency of the cell is, therefore, about 71 per cent; for comparison, the efficiency of modern steam turbines approaches 50 per cent.

The basic units of protein and lipid foodstuffs are also metabolized in the cell in such a way that their intrinsic energy is progressively released in small amounts and much of it stored in ATP until needed. In both cases, the derivatives of initial breakdown reactions are channeled into the TCA cycle for complete oxidation. The processing of amino acids, the units of protein foods, involves their deamination (loss of their $-NH_2$ groups, Fig. 2.8*J*) followed by direct conversion to certain of the intermediates of the metabolic sequences of carbohydrate metabolism. The $-NH_2$ groups are converted into ammonia (NH_3), the nitrogenous waste product of cellular metabolism. On the other hand, the fatty acids derived from lipid foods are initially handled in a more complex manner. The fatty acid, which is a long-chain hydrocarbon molecule (Fig. 2.8*E*), is degraded in the fatty acid cycle which can be compared to a spiral staircase. First, the fatty acid must be "activated" by combining with coenzyme A in the presence of ATP. Then, on each turn of the staircase, a two-carbon fragment complexed with coenzyme A and known as acetyl coenzyme A is removed from the chain. The remaining part of the fatty acid molecule is again activated by another molecule of coenzyme A, and another molecule of acetyl coenzyme A is removed. This process is repeated until the entire fatty acid is degraded. Each of the molecules of acetyl coenzyme A enters into the TCA cycle for final oxidation.

These reactions of cellular metabolism which have been described occur in animals from protozoa to man, and in plants as well. Compounds resulting from different preparatory reactions of the carbohydrates, lipids, and proteins eventually enter the TCA cycle. Here oxidation occurs, and the waste products carbon dioxide and water are formed.

Cellular metabolism includes the synthetic mechanisms of anabolism as well as the degradations of catabolism. In the cell, some of the reactions described for the degradation of food compounds may be reversed, under appropriate conditions, with the formation of a new compound necessary for the living organism as the end result. Enzymes, secretions, nucleic acids, characteristic amino acids and fatty acids as well as the proteins, lipids, and compound carbohydrates are built up or synthesized in cells. Particularly important for many synthetic reactions is coenzyme A (p. 33) and, of course, ATP.

Cell Division

When cells were first discovered, it was thought that they arose spontaneously by a sort of crystallization. The nucleus was interpreted by some early investigators as a new cell in the process of formation. As the microscope was perfected and more observations were made, new cells were found to be formed as a result of the division of previously existing cells, and in no other way. Periods of division alternate with periods during which the cell is said to be in the vegetative or nutritive stage, that is, when it is either growing or maintaining itself as a functional unit of the organism. The cell is sometimes referred to, at this time, as a resting cell, but no designation could less adequately describe it during this period of metabolic activity. After a cell has reached a certain size, it may divide. Whether or not cell size is the only factor conditioning cell division, it is certainly a very important one. The division of the cytosome is always preceded by division of the nucleus, which may occur by the method of amitosis or by mitosis.

Amitosis. In amitosis, or direct nuclear division, the nucleus becomes somewhat elongated and constricts into two parts which are about equal in volume. The nuclei of certain types of cells may divide amitotically without division of their cytosomes and thus give rise to multinucleate cells. However, the cytosome may divide after the nucleus is constricted, and two new cells are formed. The distribution of nuclear components is only approximately equal in this direct process of division. Such a type of division apparently occurs most often in cells that are very specialized, very old, or in some abnormal or degenerating condition.

Mitosis. The typical method of nuclear division is by mitosis. It is called the indirect method because it involves changes that are more complicated than the simple constriction of amitosis. The process of mitosis, which was first fully studied in animal cells by Walter Flemming in 1878, is divided for purposes of description into four continuous stages: prophase, metaphase, anaphase, and telophase.

The general structure of a vegetative cell should be recalled, with particular reference to the cell center and the nucleus (p. 21). In some cells there are two centrioles during the vegetative phase; in others, only one. For this account let us consider a cell in which two centrioles are present. Among the earliest changes to occur in the **prophase** of mitosis is the separation of the two centrioles toward opposite sides of the nucleus (Fig. 2.10). At the same time delicate fibers become visible about the centrioles in the region of the cell center. The fibers that stretch between the centrioles as they move apart are known as the **spindle fibers,** since they converge toward the centrioles in a typical spindle formation. Fibers called **astral rays** extend freely from each centriole into the surrounding cytoplasm. The structure formed by the fibers and the centrioles is known as the **mitotic spindle,** because of the arrangement of the fibers that pass from one centriole to the other. The source of the fibers and their exact nature are not clear, but the reality of the mitotic spindle is indisputable (Fig. 2.7*B*); by suitable methods it can be isolated from the cell. While the mitotic spindle is being formed in the cytosome, delicate chromatic threads appear in the nucleus and are seen to be double; that is, two threads are found close together. Around these two **genonemata,** so-called because they are apparently made up of the linearly arranged hereditary units or genes (p. 190), intensely staining chromatic material accumulates. These elements shorten and thicken forming chromosomes (Fig. 2.10). Chemically the chromosomes are known to contain desoxyribonucleic acid (DNA) and characteristic proteins. When chromosomes are gently dissociated, they are demonstrated to be composed of macromolecular granules which may be the genes, or clusters of them, held together by ionic bonds (p. 23).

Chromosomes may be different in size and shape in the cells of an organism; that is, round chromosomes and straight and bent rods occur. The shape

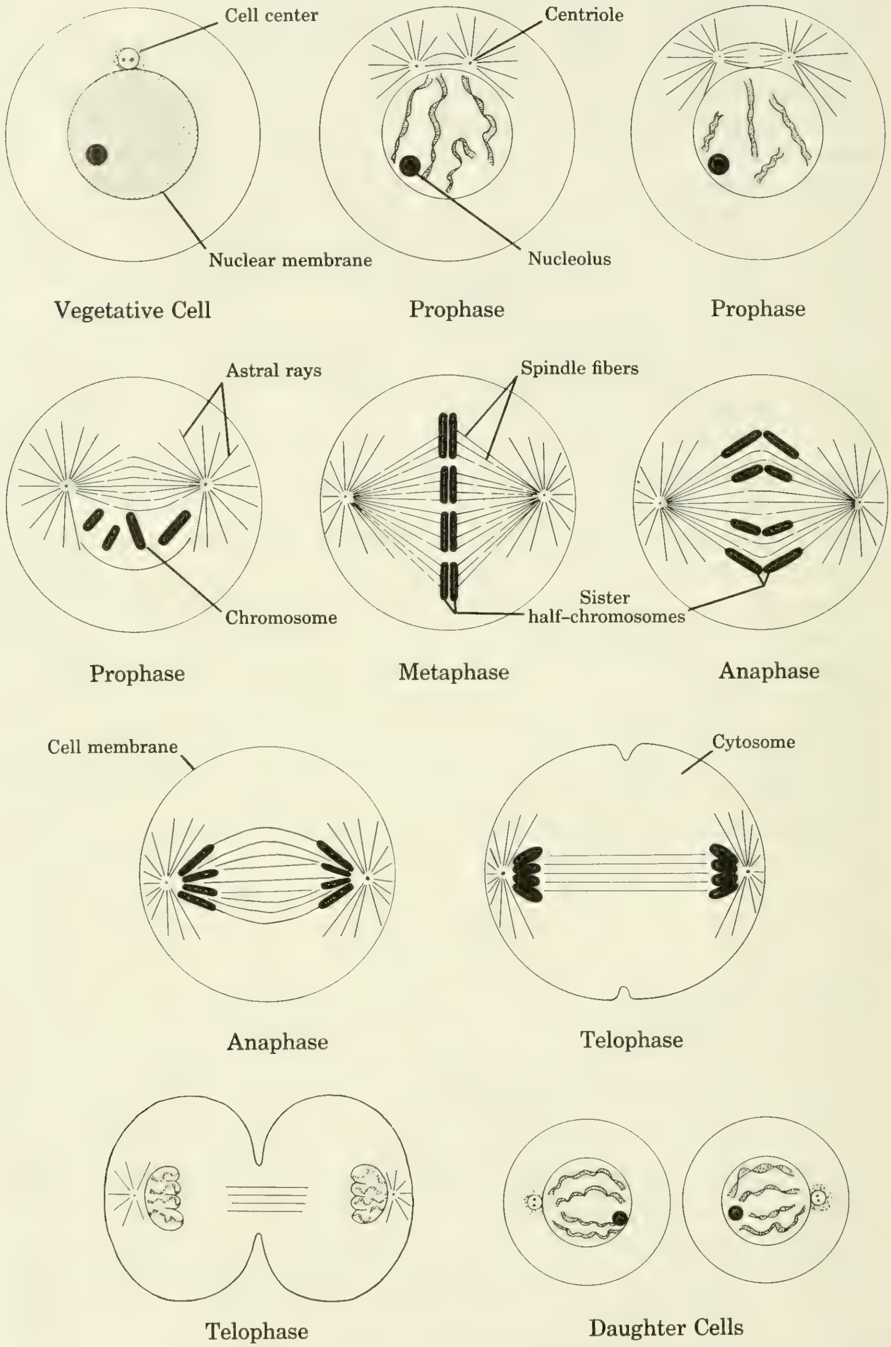

Cell center
Centriole
Nuclear membrane
Nucleolus
Vegetative Cell
Prophase
Prophase
Astral rays
Spindle fibers
Chromosome
Sister half-chromosomes
Prophase
Metaphase
Anaphase
Cell membrane
Cytosome
Anaphase
Telophase
Telophase
Daughter Cells

Fig. 2.10. Mitosis and cell division in animal cells; diagrammatic.

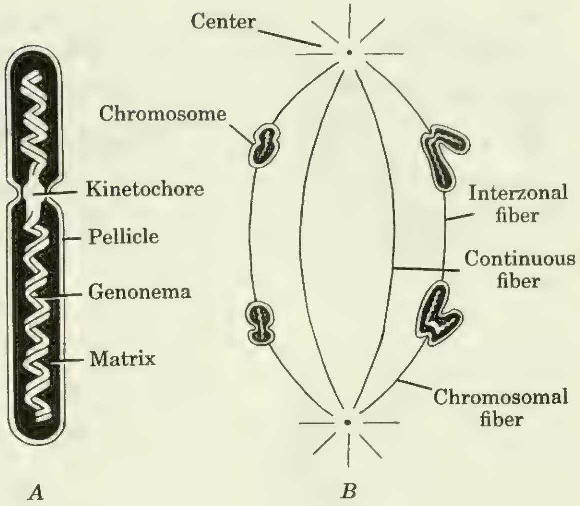


Fig. 2.11. *A*, structure of a chromosome; diagrammatic. *B*, relation of chromosomes to the mitotic spindle; diagrammatic. (Redrawn from F. Schrader, *Mitosis*, copyright 1944 by Columbia University Press, printed by permission.)

of a rod-like chromosome depends on the position of the **kinetochore**, a faintly stained region of the chromosome that becomes associated with a spindle fiber (Fig. 2.11). The kinetochore is capable of duplication and resembles the centriole in a number of respects; its structure in electron micrographs has not been reported. If the kinetochore is near the end of a chromosome, it appears straight; a subterminal or median position of the kinetochore produces a J- or V-shaped chromosome. No matter what the shapes and sizes of the chromosomes are, we find that there are two of each kind as they become fully condensed toward the end of the prophase. Two chromosomes that are alike in shape and size are known as **homologous chromosomes**. The total number of chromosomes visible at the end of the prophase is the **diploid number** characteristic of any species. In any given kind of animal or plant, the same number of pairs of chromosomes will be found in all the cells of the body, with the exception of the mature germ cells (Fig. 2.12). In some species the males have one fewer chromosomes than the females; that is, one chromosome is unpaired. This same kind of chromosome occurs as a pair in the female. Chromosomes that differ in number in the two sexes are known as **sex chromosomes** (p. 209); the other chromosomes, of which there are two of each kind in both sexes, are called **autosomes**. Coincident with the formation of the mitotic spindle and the condensation of the chromosomes, the nuclear membrane begins to disappear, first in the region next to the spindle, and the nucleolus is lost to view. The chromosomes take up a position on the spindle midway between the centrioles to form the **equatorial plate**; at this time a spindle fiber connects the kinetochore with the centriole (Fig. 2.11). These changes mark the end of the prophase. Observations on certain kinds of living cells growing in a nutrient medium (tissue-culture conditions) indicate that the changes of the prophase take about 8 minutes to occur.

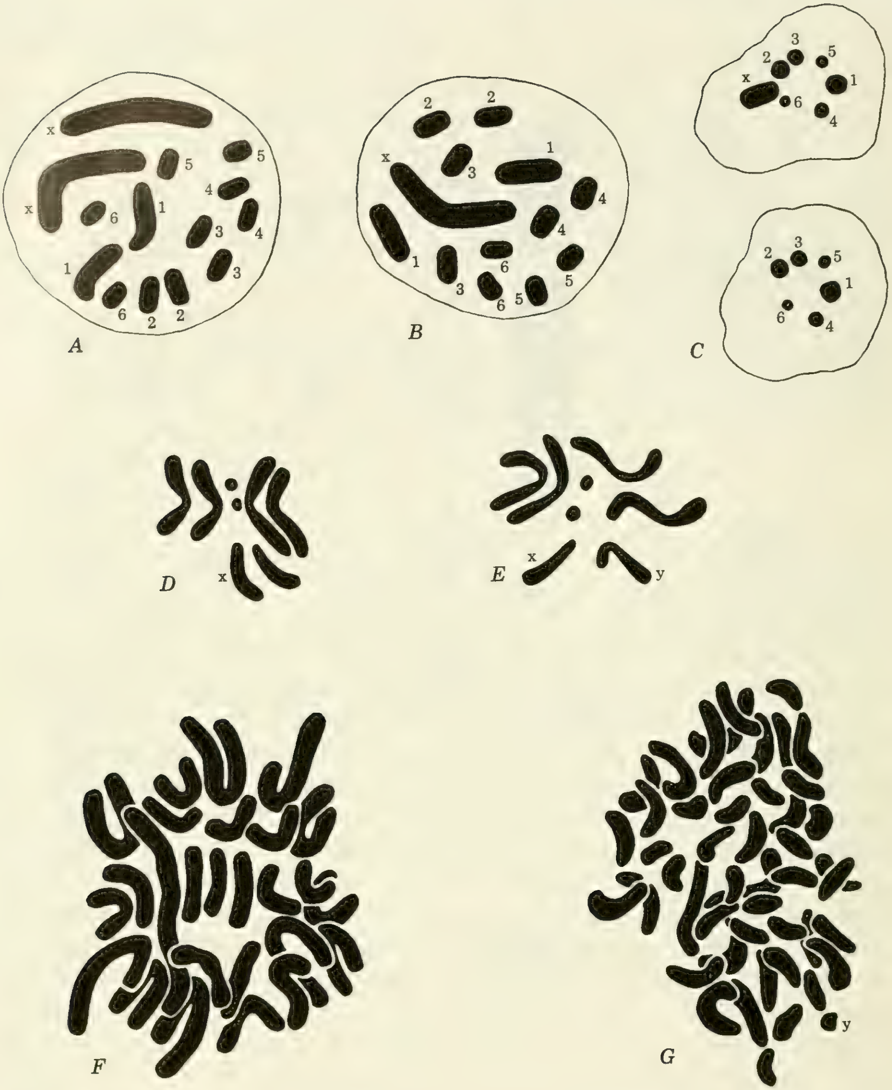


Fig. 2.12. Chromosomes from various animals. *A* and *B*, an oögonium and a spermatogonium, respectively, of the bug, *Protenor*, showing the two X-chromosomes of the female and the single X-chromosome of the male, as well as the 6 pairs of homologous autosomes; homologous members of the pairs are numbered alike: ×3600. The diploid number of chromosomes in *Protenor* is 14 in the females and 13 in the males. *C*, two spermatids of *Protenor*, one of which has received the X-chromosome at the disjunctional division; each spermatid has one chromosome from each of the pairs of autosomes: ×2900. The haploid number of chromosomes in *Protenor* is 6 in one-half of the spermatozoa, 7 in the other half of the spermatozoa and in all of the ova. *D* and *E*, female and male diploid groups from *Drosophila* in which the chromosome number is the same, 8, because the male contains a Y-chromosome: ×5500. *F*, chromosomes of an oögonium of the frog, *R. pipiens*, showing 26 as the diploid number: ×3000. *G*, chromosomes of a human spermatogonium, showing 48 as the diploid number; the Y-chromosome is labeled: ×3480. (*D* and *E*, modified from C. B. Bridges, 1916, *Genetics*, vol. 1; *F*, from C. L. Parmenter, 1925, *Journal of General Physiology*, vol. 8; *G*, from H. M. Evans and Olive Swezy, 1929, *Memoirs of the University of California*, vol. 9.)

The succeeding **metaphase** is the stage at which the longitudinally doubled chromosomes are arranged on the equatorial plate (Fig. 2.10). The duality that is such a conspicuous characteristic of a metaphase chromosome results from the separation of the matrix after the genonemata have separated from one another in the middle prophase. Each of the sister half-chromosomes in the equatorial or metaphase plate contains one of the two genonemata found in the prophase chromosome. The doubling of the chromosome in such a way that sister half-chromosomes have equivalent genonemata is of great theoretical significance (p. 190). The mechanism of distribution of chromosomes is regarded as a mechanism for the equal distribution of genes.

The beginning of the **anaphase** is indicated by the separation of the halves of each chromosome, a moving of one half-chromosome toward each centriole or pole of the spindle (Fig. 2.10). What produces this movement is still unknown, but it is initiated in the region of the kinetochore, now reduplicated. As the half-chromosomes move toward the poles, careful examination reveals that each contains two genonemata. This fact explains why two genonemata occur in each prophase chromosome; the genonemata persist from one period of division to the next. The exact time and the mechanism of replication of the genonemata remains unknown. It can be stated, however, that one genonema does not split to form two half-genonemata, each of which then reforms the part it has lost. Instead, each genonema in some way serves as a template upon which an exact duplicate is synthesized. When it is completed, this new genonema becomes free from its pattern.

As the chromosomes near the poles of the spindle, they come to lie very close to one another. This marks the beginning of the **telophase,** during which a new or daughter nucleus is formed from each clump of chromosomes (Fig. 2.10). A nuclear membrane appears at the periphery of the chromosome group at each pole, and the members of the group begin to separate. The chromatin progressively loses its capacity to stain, but not uniformly; the thread-like genonemata stain after the matrix will no longer react with a dye. Thus, the nucleus of a vegetative cell is formed, and one or more nucleoli soon make their appearance. The centriole, meanwhile, has reduplicated, and the spindle fibers begin to disappear.

While the telophase of nuclear division is occurring, constriction of the cytosome takes place in the plane of the equatorial plate of the mitotic spindle. When constriction of the cytosome is complete, cell division is finished; the entire process requires somewhat more than 30 minutes for its completion. Two cells have been formed from one by a complicated process, the most important aspect of which is the manner of distribution of the half-chromosomes, each containing equivalent genonemata. Each new cell gets exactly the same kind and amount of chromatic material. The essential significance of mitosis is the equal qualitative and quantitative distribution of the hereditary material.

When the daughter cells enter the vegetative phase, they soon grow to the size typical of their kind. It has been stated that this growth requires from 1 to 2 hours under favorable nutrient conditions. There follows a period of the activity characteristic of the particular kind of cell, and after about 12 hours mitosis may occur again, followed by cytosomal constriction. The times given here are for cells in tissue cultures; other kinds probably differ somewhat, and a variety of bodily conditions doubtless affect division rates. It should be clear that what evidence exists indicates that the chromatic threads found in each anaphase and telophase chromosome persist through the metabolic phase to the succeeding prophase, even though there is no morphological proof. The importance of this continuity of the genonemata from cell generation to cell generation will be increasingly apparent, and the changes that occur during mitosis should be clearly understood.

Summary

In this chapter we have described the structure of the cells which make up the bodies of animals and in which the vital processes occur. As we study many-celled animals, we shall find that major functions are associated with special structures—digestion with a digestive tract and glands, gas exchange with gills or lungs or air tubes, circulation with pulsating tubes and special fluids. Structure and function are intimately related to the organism as a whole, and so it is with cells.

One of the things you may have thought about as you studied the "composite cell" is that all the different parts are definitely located. Many of the structures are separated from one another by membranes, just as the entire cell is separated from other cells by its plasma membrane. These membranes are semipermeable, however, and some are porous in addition—communication is possible between the various compartments of the cell. It has been known for a long time that the chromosomes found in the nucleus of the dividing cell are the structures associated with the synthesis and transmission of the hereditary material of the cell, and so of the individual and species. In recent years, other functions of the cell have been associated with particular structures. Elucidation of the steps in cellular metabolism reveals that enzymes work as teams in carrying out the transformations of metabolism. And the inference is made that very often, perhaps always, the members of these teams occupy definite positions with reference to one another; space relations are important in chemical reactions. Insoluble enzymes involved in cellular oxidation are known to be located on the mitochondrial membrane; soluble ones are in its matrix.

The great expanse of lipoprotein membrane in the endoplasmic reticulum, together with the obvious possibility for precise spacing of enzymes on it—like traffic directives painted on a highway—and its typical association with the RNA "messengers" from the nucleus open up stimulating vistas for scientific imagination and research. Biological science has stepped over a threshold into a period of exciting revelations concerning the microcosm we call the cell.

CHAPTER 3

METABOLISM

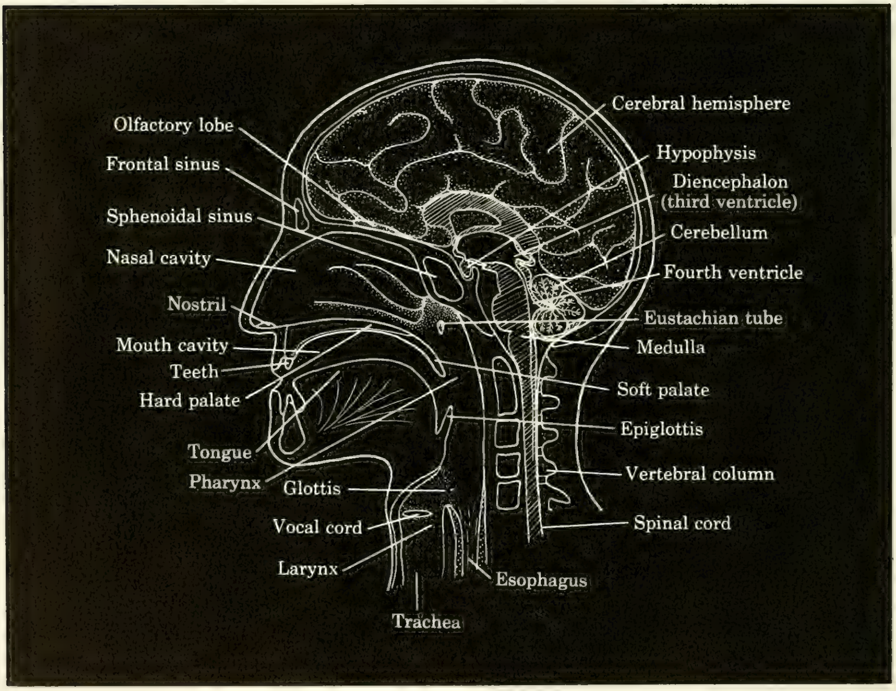

Olfactory lobe
Frontal sinus
Sphenoidal sinus
Nasal cavity
Nostril
Mouth cavity
Teeth
Hard palate
Tongue
Pharynx
Glottis
Vocal cord
Larynx
Trachea
Esophagus
Cerebral hemisphere
Hypophysis
Diencephalon (third ventricle)
Cerebellum
Fourth ventricle
Eustachian tube
Medulla
Soft palate
Epiglottis
Vertebral column
Spinal cord

Fig. 3.1. The human head, shown as if cut in the median longitudinal plane; semidiagrammatic.

IN VERTEBRATES

If we recall the metabolic requirements of individual cells, we can immediately grasp the fact that the problems of maintenance and growth in many-celled animals must be complex. Living cells must be bathed with a continuous supply of essential nutrients and oxygen and be kept clean, so to speak, through a continuous removal of waste products of their living. Analogies can be drawn between the needs of a community of cells and those of a community of human beings. Let us, instead, undertake a scientific analysis of the way in which vertebrates, like ourselves, manage to live. We shall do this by first looking at the structure or morphology of these animals with special reference to the parts related to maintenance problems. Most of you are dissecting a vertebrate animal, such as the frog, in the laboratory; the brief discussion of vertebrate structure here is only intended to highlight the information you already have. Major emphasis will be on the kinds of individual tissues that exist in a vertebrate and especially on the way in which the tissues and organs function.

We shall see that cells are specialized to form tissues and that special arrangements of these form the organs of the various anatomical divisions or systems of the body. The **organ systems** to be considered in this chapter are: (1) the digestive system, (2) the circulatory system, (3) the respiratory system, and (4) the excretory system.

Organ Systems Related to Metabolism

The Digestive System. The digestive system is made up of the **digestive tract**, which is a tube, and the attached digestive glands, the **liver**, the **pancreas**, and, in many vertebrates, the **salivary glands**. The digestive tract is, in effect, a tunnel through which food passes as it is digested or chemically changed for use by the cells of the body. Through the lining of certain parts of the tract, substances actually enter the body by absorption. The parts of the tract are the **mouth cavity, pharynx, esophagus, stomach, small intestine,** and **large intestine.**

Teeth and **tongue** are characteristic structures of the mouth cavity, although birds do not have teeth (Fig. 3.1). **Salivary glands** empty their product, the **saliva,** into the mouth cavity in terrestrial vertebrates by way of the **salivary ducts** (p. 61). The **mouth,** or opening of the mouth cavity, is the place of food intake or **ingestion,** and teeth either hold the food in the mouth cavity or initiate its mechanical breakup. Various functions are performed by the tongue in different vertebrates: in frogs and lizards it serves to capture food; in mammals it functions to manipulate food, as a site for the taste buds (p. 110) and, in man, as an important adjunct to speech.

No obvious landmark separates the mouth cavity and pharynx; they bear different names because of the manner of their origin during development. Both serve jointly as passageways for food and air. During evolution an important change occurred in these regions, as can be seen by comparing man with the frog. In man a horizontal partition, the **hard palate,** separates off an upper portion of the original undivided mouth cavity, such as is found in the frog. This upper part, the **nasal cavity,** opens externally by the **nostrils** and is exclusively an air pathway (Fig. 3.1). Posteriorly, the nasal cavity is continuous with the **nasal pharynx,** which is only incompletely separated from the **oral pharynx** by the **soft palate.** On each side the **Eustachian tube** leads from the anterior part of the pharynx to the cavity of the middle ear (Fig. 4.4, p. 90). Posteriorly, the pharynx is continuous with the esophagus and, ventrally, connects with the air passages through a slit-like opening, the **glottis.** This crossing, so to speak, of the food and air paths is not a very efficient arrangement, as everyone is well aware.

The esophagus varies in length with the neck of the vertebrate. Usually, it only carries the food from the pharynx to the stomach, but in birds a part of it, the **crop,** is expanded to serve for food storage. In some mammals, such as the ruminants, expanded regions of the esophagus form part of what is ordinarily referred to as the "stomach," again functioning as a storehouse of food.

The stomach and the small intestine, which are distinctly separated by the **pyloric sphincter,** are essentially comparable in structure in all vertebrates. They, together with the large intestine, are suspended in the **coelom,** or body cavity, by the **mesenteries.** These are formed by two layers of the **peritoneum** which lines the coelom and covers the stomach and intestines (p. 69). The mesenteries serve to anchor the gut and to hold the liver, pancreas, and spleen. Mesenteries function as bridges by means of which the blood and lymph vessels, as well as nerves, reach the organs of the body cavity; they are also important fat depots (p. 77).

The coelom has only two compartments in the lower vertebrates such as the frog, the **pericardial cavity,** containing the heart, and the **pleuroperitoneal cavity.** In mammals this cavity is divided into three, two **pleural cavities,** each con-

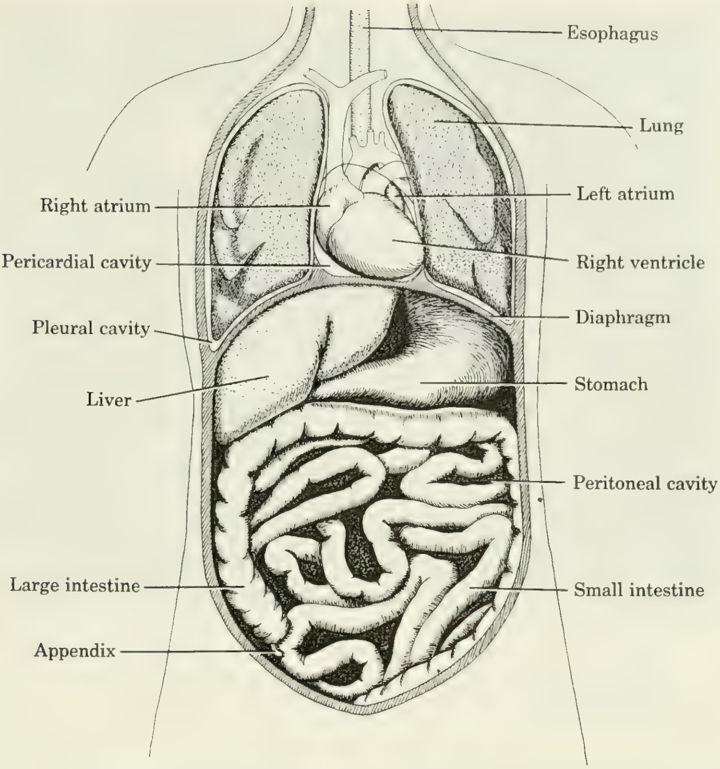

Esophagus
Lung
Right atrium
Left atrium
Pericardial cavity
Right ventricle
Diaphragm
Pleural cavity
Stomach
Liver
Peritoneal cavity
Large intestine
Small intestine
Appendix

Fig. 3.2. The coelomic cavities and coelomic viscera of man.

taining a lung, and the **peritoneal** or **abdominal cavity** (Fig. 3.2). The pericardial cavity lies between the two pleural cavities; these three cavities occupy the chest or thoracic region of the trunk of the body. The peritoneal cavity is located in the abdominal part of the trunk. It is here that the stomach, small and large intestine, liver, and pancreas are found.

Different degrees of folding and papillation occur in the stomach and small intestine in the different groups of vertebrates, related to increase of the surface of the lining epithelium. Various digestive glands are in the lining, and it is the absorptive surface. In the small intestine, there is marked variation in the length which is correlated with the diet; the more concentrated the diet, the shorter the small intestine. In the frog tadpole, which eats a plant diet, the intestine is about 20 inches long, as compared with 12 inches in the insect-feeding adult. Carnivorous mammals have shorter small intestines than herbivorous ones, many of which have pouch-like outgrowths, or **caeca**, correlated with retention of large quantities of low-calorie plant food. The rudiment of such a caecum occurs in man near the junction of the small and large intestine; it is known as the **appendix**.

The liver and pancreas originate from the embryonic gut and remain at-

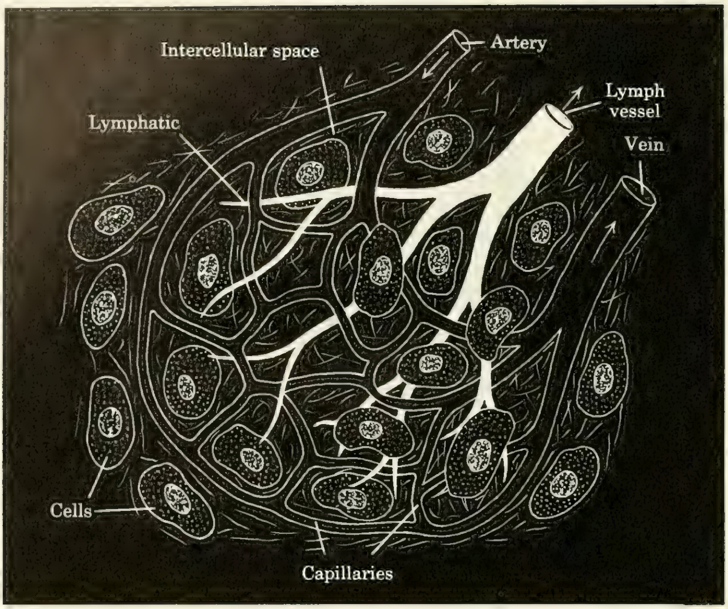


Fig. 3.3. The capillaries and lymphatics in relation to cells throughout the body; diagrammatic. The arrows indicate the direction of circulation.

tached to that part which becomes the anterior portion of the small intestine, or **duodenum**, by way of their ducts, the **bile duct** and the **pancreatic duct**, respectively.

The large intestine is very short in the frog, but it is quite conspicuous in mammals, including man, and is separated into the **colon** and **rectum**, which opens externally by way of the **anus**. In most of the vertebrates, as in the frog, the large intestine is not differentiated into regions. It opens into the **cloaca**, which is a common passageway for substances coming from the excretory organs and urinary bladder, for germ cells from the reproductive organs, as well as for material from the large intestine. The external opening of the cloaca is the anus. When, in the evolution of mammals, the cloaca was divided into a ventral urino-genital sinus and a dorsal rectum, a new opening was formed ventrally; the term anus is retained for the opening through which materials leave the digestive tract.

The Circulatory System. All the cells of the vertebrate body have, in spite of its complexity, a common internal environment. This is so because of the circulating fluids of the body, the **blood** and **lymph**, carried to all parts of the body by the **circulatory system**. This system is divided into the **blood-vascular system** and **lymphatic system**, depending on the type of fluid carried.

The blood-vascular system of vertebrates is, with few exceptions, what is known as a closed system. That is, as the blood courses through the body, it is confined to definite channels, in contrast to the situation in many, but not all, invertebrates. The chief parts of the blood-vascular system are the same in all vertebrates. There is a highly muscular region known as the **heart**, located in the pericardial cavity (Fig. 3.2). By contracting rhythmically, beating as we say, the heart forces the blood into the **arteries**, or vessels in which blood flows away from the heart. Arteries divide repeatedly as they pass to all parts of the body and finally end in a network of very thin-walled, small vessels known as **capillaries**, which are found in all organs of the body in close association with the cells (Fig. 3.3). The capillaries are also connected with other larger vessels, known as **veins**, through which the blood flows toward the heart. The arteries and veins that are seen when a vertebrate animal like the frog is dissected are, therefore, continuous with each other in organs all over the body by way of the capillaries. There is one very important exception to this statement in all vertebrates. Blood leaving the capillaries of the stomach and intestine passes into what is known as a **portal vein** because it carries the blood to another set of capillaries. This portal vein is called the **hepatic portal vein** because the capillary bed which it feeds is located in the liver. In lower vertebrates there is a second portal system; blood returns from capillaries in the hind legs to capillaries in the excretory organs by way of the **renal portal veins.**

The heart connects the veins and arteries, so that the blood flows continuously away from the heart in the arteries, into the capillaries, thence into the veins, and so back to the heart. Although this statement describes a very simple circuit, such as that in the fishes, it is essentially true for all vertebrates. The differences that exist in the circuits of the different kinds of vertebrates are related to changes that occur in the heart and in some of the larger arteries and veins (Figs. 3.4, 3.5, and 3.6). In vertebrates with lungs, it is convenient to refer to the arteries and veins that supply regions of the body other than the lungs as **systemic** arteries and veins, in contrast to **pulmonary** arteries and veins supplying the lungs.

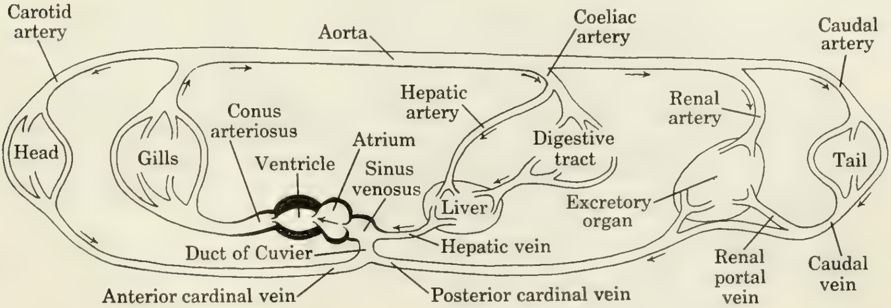

Carotid artery
Aorta
Coeliac artery
Caudal artery
Hepatic artery
Renal artery
Conus arteriosus
Atrium
Head
Gills
Ventricle
Sinus venosus
Digestive tract
Tail
Liver
Excretory organ
Hepatic vein
Duct of Cuvier
Renal portal vein
Caudal vein
Anterior cardinal vein
Posterior cardinal vein

Fig. 3.4. The circulatory system in a vertebrate having a heart with one atrium and one ventricle, as in elasmobranch fishes; diagrammatic. The arrows indicate the direction of circulation.

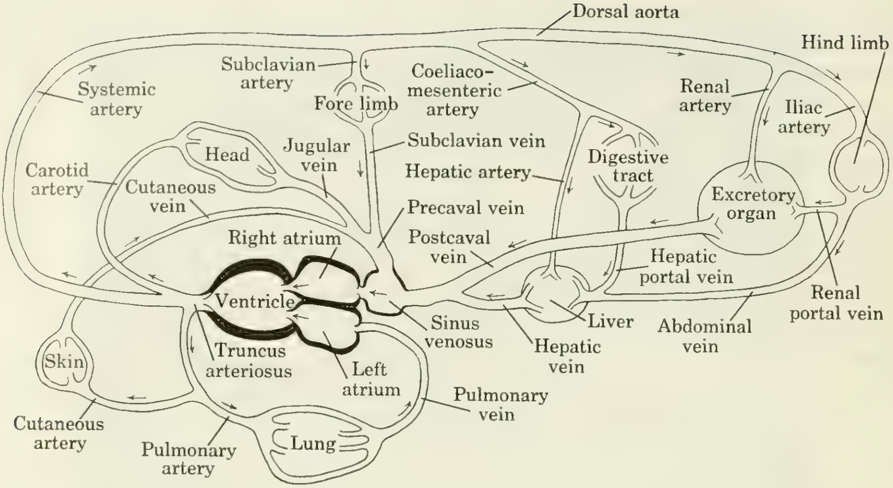

Dorsal aorta
Hind limb
Subclavian artery
Coeliaco-mesenteric artery
Systemic artery
Fore limb
Renal artery
Iliac artery
Head
Jugular vein
Subclavian vein
Carotid artery
Cutaneous vein
Hepatic artery
Digestive tract
Excretory organ
Precaval vein
Right atrium
Postcaval vein
Hepatic portal vein
Ventricle
Sinus venosus
Liver
Abdominal vein
Renal portal vein
Skin
Truncus arteriosus
Left atrium
Hepatic vein
Pulmonary vein
Cutaneous artery
Pulmonary artery
Lung

Fig. 3.5. The circulatory system in a vertebrate having a heart with two atria and one ventricle, as in the frog; diagrammatic. The arrows indicate the direction of circulation.

The arrangement of the chambers of the heart and its valves controls the direction of blood flow as the heart contracts (Figs. 3.7 and 3.8). Blood leaving the heart enters the large arteries which have walls sufficiently heavy to maintain a fairly constant diameter; their walls contain, in addition to the thin lining of endothelium, elastic connective tissue, and non-striated muscle. As the arteries divide and redivide, the bore of each branch becomes smaller and the wall thinner. Of course, the total capacity or volume of the branches is far greater than that of the original artery. Capillaries are limited only

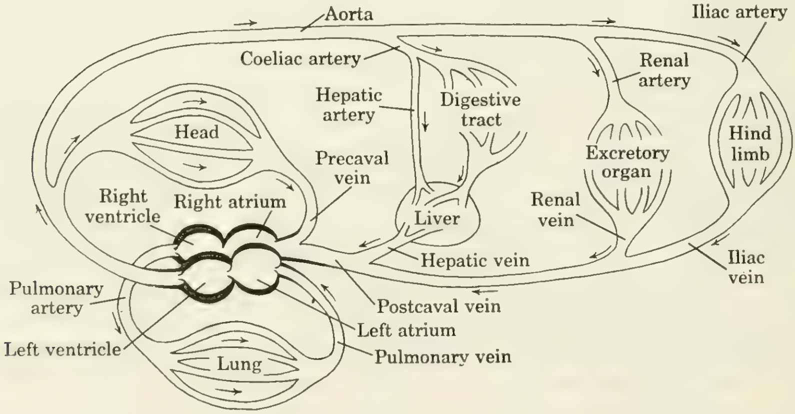

Aorta
Iliac artery
Coeliac artery
Renal artery
Hepatic artery
Digestive tract
Head
Hind limb
Excretory organ
Precaval vein
Right ventricle
Right atrium
Liver
Renal vein
Hepatic vein
Iliac vein
Pulmonary artery
Postcaval vein
Left atrium
Left ventricle
Lung
Pulmonary vein

Fig. 3.6. The circulatory system in a vertebrate having a heart with two atria and two ventricles, as in mammals; diagrammatic. The arrows indicate the direction of circulation.

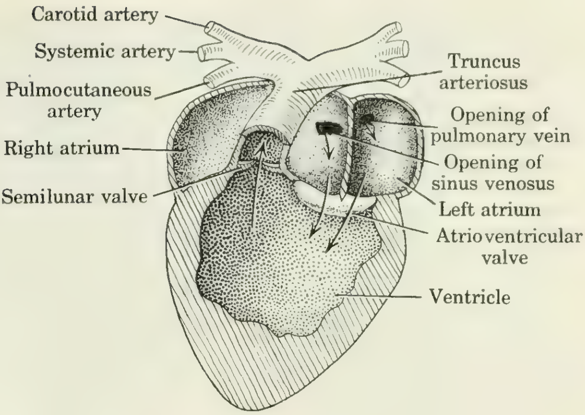

Carotid artery
Systemic artery
Pulmocutaneous artery
Right atrium
Semilunar valve
Truncus arteriosus
Opening of pulmonary vein
Opening of sinus venosus
Left atrium
Atrioventricular valve
Ventricle

Fig. 3.7. Heart of the frog, with the ventral walls of the ventricle and atria removed. The arrows indicate the direction of circulation.

by the endothelium, and continued branching increases the capacity of the bed over that of the small arteries feeding it. All this is significant in connection with blood pressure and its rate of flow. When the heart contracts, a quantity of blood is suddenly forced into an artery which has much less capacity than the ventricle. The blood pressure in the aorta of man in a normal resting state is 90–100 mm. of mercury. As the cross-sectional area of all the branches increases, that is, as the capacity of the vessels increases, the blood pressure drops until it is only about 25–30 mm. of mercury as it enters the capillary bed. Here, the pressure falls still more, down to about 15 mm. of mercury, and the blood moves relatively slowly; this is important in connection with the exchanges that occur between blood and cells in capillary beds. Veins have walls containing some non-striated muscle in addition to the endothelial lining but have little ability to resist expansion; hence, the

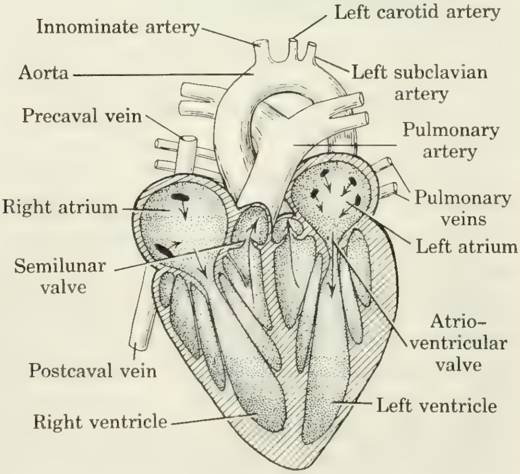

Innominate artery
Left carotid artery
Aorta
Left subclavian artery
Precaval vein
Pulmonary artery
Right atrium
Pulmonary veins
Left atrium
Semilunar valve
Atrio-ventricular valve
Postcaval vein
Left ventricle
Right ventricle

Fig. 3.8. Heart of man, with the ventral walls of the ventricles and atria removed. The arrows indicate the direction of circulation.

pressure in the veins is lower than it is in arteries. Movement of blood toward the heart from the lower extremities of upright vertebrates such as man is aided by valves in the veins of the legs. During movement of the legs, the contraction of the skeletal muscles (p. 68) helps to push the blood along, with the valves preventing backflow.

The heart beats about 70 times per minute in a normal resting man. At each contraction, a pulse wave moves along the arterial wall and can be felt in any large peripheral artery. However, this pulse wave moves much faster than the blood. By means of radioactive particles inserted in a peripheral vessel, it can be shown that it takes 20 to 25 seconds for blood to repass the point of insertion, that is, for a complete trip through the body. About 5 liters of blood leave the heart every minute during normally quiet living. If you realize that the cardiac output is greatly increased during muscular exercise, up to 30 liters per minute, and think of the years that the human heart can function continuously, you will begin to appreciate what an amazing organ it is. The mechanism and control of this remarkable pump will be described later (p. 117).

In spite of the fact that the pressure of the blood in the capillary is relatively low, some filtration of the blood plasma occurs through the single-celled wall, in addition to diffusion. Some white blood cells may also move out between the cells of the lining. Thus, a fluid bridge is formed between the contents of the capillary and the nearby cells; this fluid is called the **interstitial fluid** or **lymph**. Some of it apparently re-enters the capillaries as the pressure decreases in the bed, but much of it enters the closed terminal vessels of the **lymphatic system** (Fig. 3.3). These **lymphatics**, as they are called, remain thin-walled as they unite to form larger vessels which eventually empty into large veins in the region of the neck in higher vertebrates. Lymph is returned from the hind legs and trunk in a fairly large channel known as the **thoracic duct**. In birds and mammals, the lymphatics pass through the **lymph nodes** where lymphocytes are differentiated and enter the lymph (p. 66). The lymph nodes are also important organs of body defense since foreign materials, such as bacteria and venoms, are filtered out there and destroyed by macrophages (p. 64). Contraction of muscles in all parts of the body moves the lymph through its thin-walled vessels, and valves control the direction of movement.

The general function of the circulating fluids as what we may call a **common carrier** will become clear as the discussion progresses. The several phases of this general function are as follows: (1) to carry necessary food materials and oxygen to the cells; (2) to carry the waste products of metabolism away from the cells; (3) to transfer hormones, or internal secretions (p. 95), from one part of the body to another; and (4) in warm-blooded animals, like the mammals, to transfer heat from regions of high oxidation and so aid in the maintenance of a constant body temperature (p. 125).

The Respiratory System. Respiratory organs are of two kinds: **gills** in water-dwelling vertebrates and **lungs** in land dwellers. Gills are tufted or

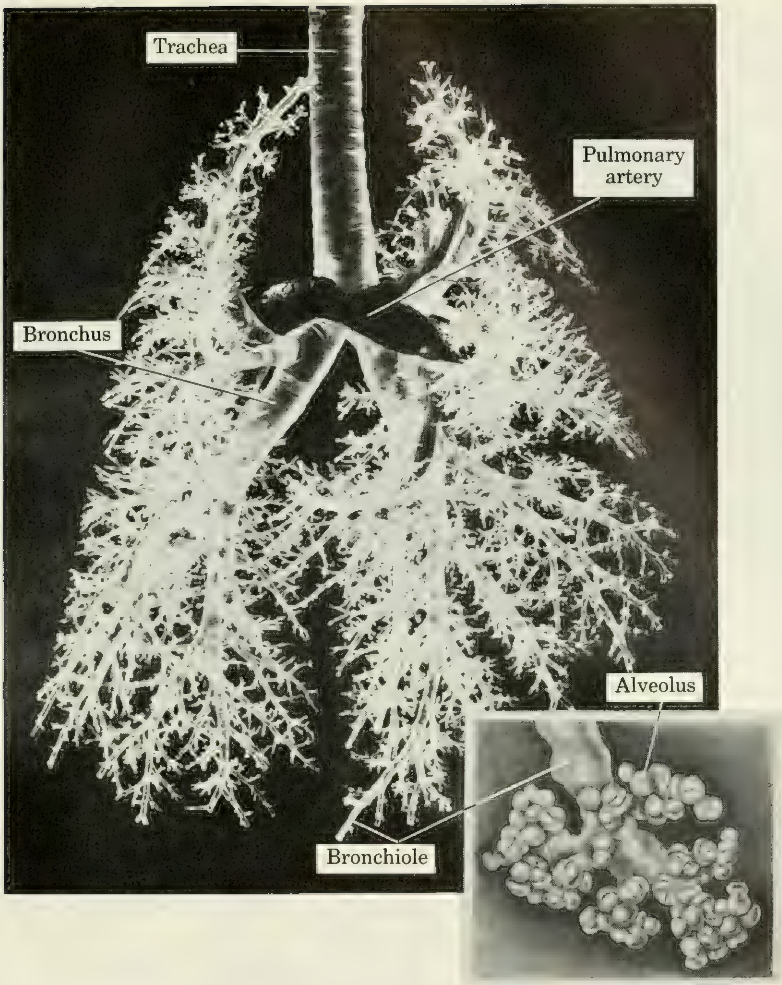


Fig. 3.9. Trachea, bronchi, and air passages of the lung in a mammal. (Photograph of plastic cast of the air passages of the lungs courtesy Ward's Natural Science Establishment.)

laminated outgrowths found along the sides of the pharyngeal pouches in fishes and some amphibians (see Fig. 5.31, p. 169). They are covered by a very thin layer of cells beneath which is a rich capillary bed. Lungs lie deep in the body and are connected to the pharynx by **air passages**; the lungs and air passages comprise the **respiratory system.**

The opening from the pharynx into the **larynx**, an expanded portion of the air passages containing the **vocal cords**, is known as the **glottis.** A tube called the **trachea** passes, alongside the esophagus, from the larynx into the chest, or thorax. There, the trachea divides into two **bronchi** which enter the lungs.

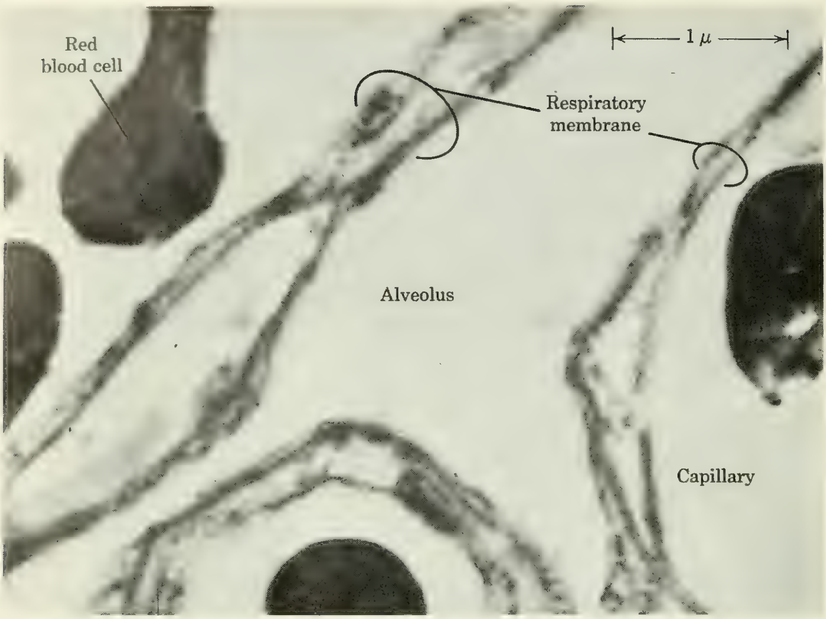


Fig. 3.10. Electron micrograph of a section through lung of rat; ×26,000. (From the original of Fig. 5, Frank N. Low, *Anatomical Record*, vol. 117, p. 257, printed by permission of the author and publishers.)

The larynx, trachea, and bronchi are prevented from collapsing by cartilaginous supports in their walls (p. 61).

Lungs in lower vertebrates such as the frog are sac-like, with the inner respiratory surface area increased by a series of folds of the lining membrane. In higher vertebrates, such as man, the bronchi branch repeatedly in the lungs forming **bronchioles**; in the smaller bronchioles cartilaginous rings are no longer present. These air passages end in small expansions known as the **alveoli** or air chambers (Fig. 3.9). Each alveolus is lined by a single layer of cells and, as in the gill, this rests on a rich capillary bed (Fig. 3.10).

In the frog the lungs lie in the **pleuroperitoneal** portion of the coelom. In the course of evolution in the vertebrates, this cavity becomes partitioned by a muscular structure known, in mammals, as the **diaphragm** (Fig. 3.2). Now, each lung lies in a closed **pleural** cavity, one on each side of the heart, surrounded by the thoracic cage (p. 92). Breathing is the result of increasing and decreasing the volume of the pleural cavities by movements of the diaphragm and ribs. The control of this mechanism will be discussed later (p. 124).

The Excretory System. The lungs, the skin, the liver, and the excretory organs are organs in which excretion occurs, but they do not make up a system of organs in the ordinary meaning of the phrase. In dividing the body into systems, it is convenient to assign a particular function to a single group or system of organs. For that reason, the lungs are discussed as part of the respiratory system, the skin as part of the integumentary system, which functions as a covering for the body, and the liver as part of the digestive system. The excretory organs and their ducts are, however, referred to as the **excretory** or **urinary system.** Since the ducts of the excretory organs are also used for the passage of male reproductive cells in vertebrates like the fishes and amphibians, the excretory and reproductive organs are frequently referred to as the **urinogenital system.** We shall not be concerned here with this dual system but shall describe the structure of the urinary system.

Two different kinds of functional excretory organs, distinguished by their manner of origin during development, are found in adult vertebrates. The first of these, the **mesonephros,** is present in adult fishes and amphibians. It appears and disappears during the development of reptiles, birds, and mammals, in which a **metanephros** is formed and functions as the excretory organ of the adult. Although both mesonephroi and metanephroi are often called **kidneys,** the term should be reserved for metanephroi. The excretory organs are paired structures located behind the peritoneum on the dorsal wall of the coelom and not suspended in it like the stomach and intestine. In mammals a **urinary bladder,** or reservoir where urine is stored before it is voided, is connected with the kidney by the **ureters** or **excretory ducts** (Fig. 3.11).

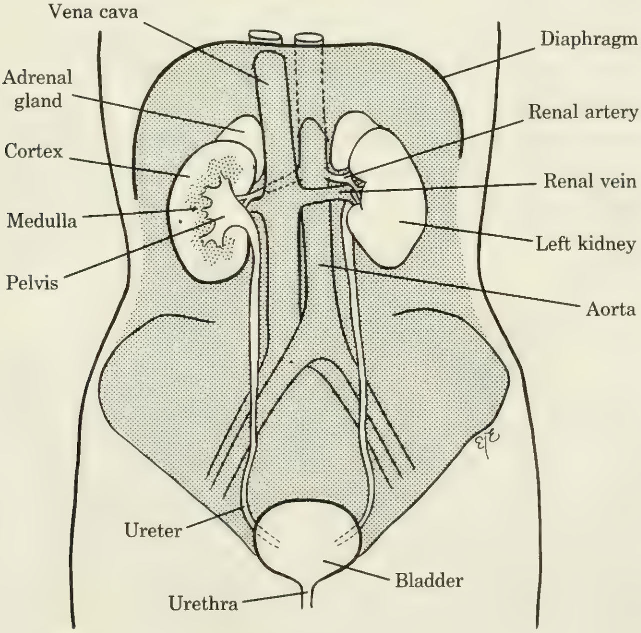


Fig. 3.11. Excretory system and related structures of man.

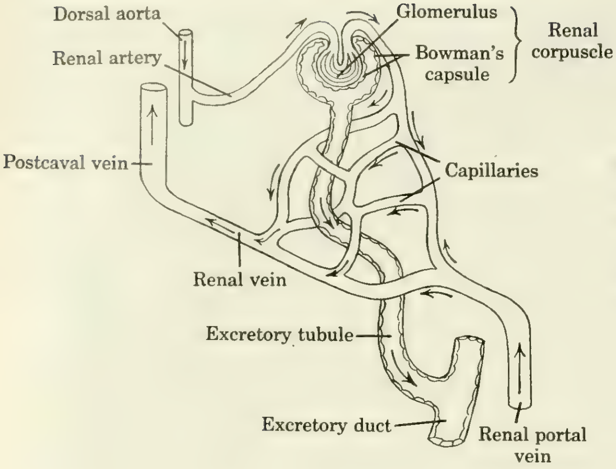


Fig. 3.12. Nephron and blood vessels in the excretory organ of the frog; diagrammatic. The nephron of man is longer and highly convoluted; there is no renal portal vein.

Inside the kidney, the ureter expands to form the pelvis of the kidney into which many small tubules empty. These carry urine from the very numerous **nephrons** or **excretory tubules** to the pelvis. Each nephron ends in a cup known as **Bowman's capsule** which contains capillaries that arise from branches of the renal artery (Fig. 3.12). Each of these groups of capillaries is a **glomerulus**, which with its surrounding Bowman's capsule makes up a **renal corpuscle.** The excretory tubules are lined by a single layer of cells and surrounded by a very conspicuous capillary network. In the frog these capillaries are fed by the renal portal vein as well as by the renal arteries, but there is no renal portal vein in mammals.

This completes the very brief survey of the morphology of the organ systems concerned with satisfying the metabolic requirements of the cells of the vertebrate. It is time now to become acquainted with the different kinds of cells found in the vertebrate body.

The Kinds of Tissues: Histology

The various systems of the body, or soma, are made up of cells, collectively known as the somatic cells. In Chapter 2 a so-called composite cell was described (p. 17). If the body of a vertebrate is examined microscopically, no cell will be found that conforms to that account; cells differ among themselves, although they all possess certain features in common. Cells may be dissimilar in shape, position in the body, structure, and also function. Cells that are similar in structure and function make up groups known as tissues; **tissues** are groups of cells specialized in the same way for the performance of the same function. Tissues are associated to form the **organs** that perform special functions. The cells as they are grouped to form tissues and organs must be studied by means of the microscope. This particular study of structure is known as **histology,** or microscopic anatomy, in contrast to gross anatomy, or the study of the organ systems by dissection. If we consider tissues first, we find that they are classified according to structure and function. There are five principal classes of tissue: epithelial, sustentative, vascular, contractile, and nervous.

Epithelial Tissue. The cells of epithelial tissues are compactly placed with but a small amount of intercellular material. Their functions include the covering and protection of body surfaces, both internal and external, as well as absorption, secretion, and excretion. According to the predominating shape of the cells, this class is subdivided into **squamous** and **columnar epithelium,** each of which is again divided into **simple** or **stratified,** depending on whether it exists in single or multiple layers. The cells of simple squamous epithelium when viewed from the surface resemble tiling blocks; seen from the edge, they are very thin (Fig. 3.13*A*). Such epithelium is found lining the coelom; that is, it forms the peritoneum (Fig. 3.13*B*). In stratified squamous epithelium only the outermost layers are typically flattened cells; in the deeper layers the cells are progressively more cuboidal (Fig. 3.13*C*). Since blood vessels do not penetrate epithelial layers, only the cells of the deeper layers

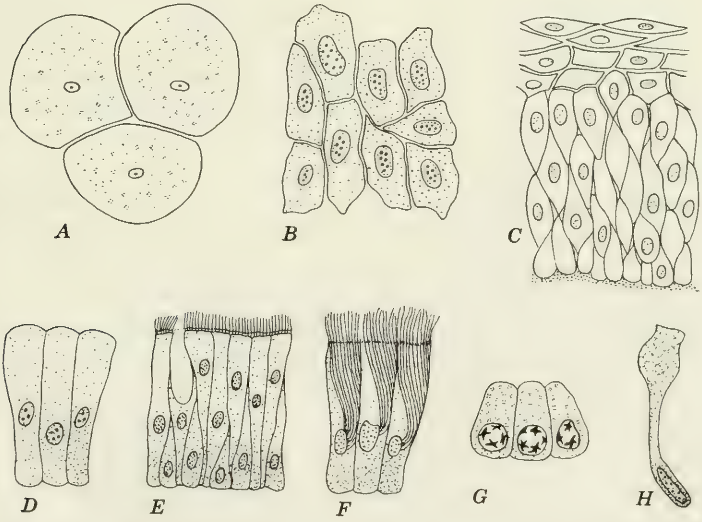


Fig. 3.13. Epithelial tissues. *A*, simple squamous epithelium from the human mouth. *B*, simple squamous epithelium (mesothelium) from peritoneum. *C*, stratified squamous epithelium from the lining of the nasal cavity. *D*, simple columnar epithelium from the mucous membrane of the digestive tract. *E*, pseudostratified ciliated columnar epithelium from the lining of the trachea; one cell is shown secreting a drop of mucus. *F*, simple ciliated columnar epithelium. *G*, glandular epithelium from the pancreas. *H*, goblet cell with a drop of mucus. *A* and *B*, surface views; *C–H*, sections at right angles to surfaces which are toward the top of the page. (*A*, *B*, and *C* from drawings by D. F. Robertson.)

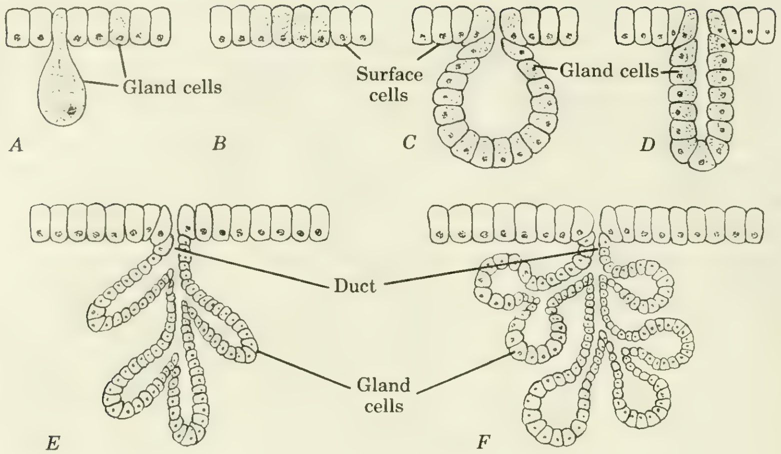


Fig. 3.14. Diagrams of glands. *A*, unicellular glands; the one at the left is shown extending below the surface layer of cells. *B*, a group of gland cells that remain in the surface layer. *C*, a simple alveolar gland. *D*, a simple tubular gland. *E*, a compound tubular gland. *F*, a compound alveolar gland.

receive abundant nourishment and consequently divide and replenish the outer layers, which die and are cast off. Stratified squamous epithelium is found in the outer layer, or epidermis, of the skin (Fig. 3.25, p. 83) and in the lining of the nasal and mouth cavities, pharynx, and esophagus of many vertebrates. In simple columnar epithelium, such as that lining most of the digestive tract, the cells are longer than they are wide and are arranged side by side (Fig. 3.13*D*). Stratified columnar epithelium is not common, but a modified type is found lining the trachea (Fig. 3.13*E*). Columnar epithelial cells sometimes have their free surfaces, that is, the surfaces exposed to the cavity they line, covered with cilia, which are very delicate cytoplasmic processes (Fig. 3.13*E* and *F*). The cilia are vibratile, and their motion removes any foreign materials from the surfaces or creates currents in adjacent fluids. The epithelium of the air passages in higher vertebrates and of the roof of the frog's mouth is an example of this variation. In the iris and retina of the eye (Fig. 4.3, p. 89, and Fig. 4.14, p. 106), epithelial cells contain pigment granules and are known as pigmented epithelium. Glands are organs essentially composed of simple columnar epithelium known as glandular or secretory epithelium (Fig. 3.13*G*). These cells have the capacity to synthesize substances, such as enzymes or hormones, that must be present in order for specific events to occur. Such substances are called **secretions.** Glands may be unicellular, as the goblet cells of the intestinal epithelium (Fig. 3.13*H*), or multicellular (Fig. 3.14). All glands begin their formation on surfaces of the body and usually sink below the surface. In doing so they may form simple **tubular glands** or become flask-shaped to form simple **alveolar glands,** such as are found in the skin of the frog. Both types of simple glands may become compound by the formation of outpocketings along their lengths. The glands related to digestion, and many others, are divided into secretory portions and the tubes, or **ducts**, by way of which the secretion passes out to the cavity or surface where it is used. Not all glands possess ducts; those that do not, the ductless glands, will be discussed in the next chapter (p. 95). The gastric glands, present in the mucous membrane of the stomach, and the intestinal glands that occur in the mucous membrane of the duodenum are simple tubular glands. The liver is a compound tubular gland; the pancreas, a compound alveolar gland.

Sustentative Tissue. The sustentative tissues, often called the connective tissues, are a very heterogeneous group, classed together because they are all derived during development from the same source—the stellate mesenchyme cells (Fig. 3.15*B*). In general, sustentative tissues function in supporting the body and connecting or binding together its parts. This group of tissues is characterized by the large amount of intercellular material produced by the cells. In the vertebrates this intercellular material is responsible for the supporting and connecting qualities. Sustentative tissue may be divided into four subclasses: connective tissue in the restricted sense, cartilage, bone, and adipose tissue.

Connective tissues are of three kinds: **mucous connective tissue,** in which the intercellular material is gelatinous, is found in the umbilical cords of mammals (Fig. 3.15*A*); **reticular connective tissue,** in which there is a meshwork of connective tissue cells with the interspaces filled with other types of cells, forms the framework of organs like the spleen (Fig. 3.15*C*); and **fibrous connective tissue,** in which the intercellular material is composed of fibers, is distributed widely as a binding tissue in many organs. The intercellular fibers of fibrous connective tissue are of two kinds, collagenous and elastic. The **collagenous** or **white fibers** are very fine and occur in bundles, whereas **elastic** or **yellow fibers** are thicker and occur singly. Fibrous connective tissue in which both collagenous and elastic fibers occur is found in the submucosa of the digestive tract and in the dermis of the skin (Figs. 3.15*D* and 3.25). Fibrous connective tissue in which collagenous fibers predominate is found in tendons, and that containing chiefly elastic fibers is found in the walls of larger arteries and in certain ligaments (Fig. 3.15*E*). The cells of fibrous connective tissues are spindle-shaped or irregular in outline and possess relatively little cytoplasm.

The second subclass of sustentative tissues is **cartilage,** which is a supporting tissue. The intercellular material in cartilage is sometimes hardened by impregnation with inorganic salts, chiefly those of calcium. Here the cells are more or less rounded and lie in spaces known as **lacunae.** When the **matrix** between the cells is translucent and apparently structureless, the tissue is called **hyaline cartilage** or gristle (Fig. 3.15*G*). Hyaline cartilage is found at the ends of long bones, at the ends of ribs, and in the cartilages of the nose and trachea. The cartilage of the external ear contains elastic fibers in its matrix and, therefore, is known as **elastic cartilage** (Fig. 3.15*H*); that found

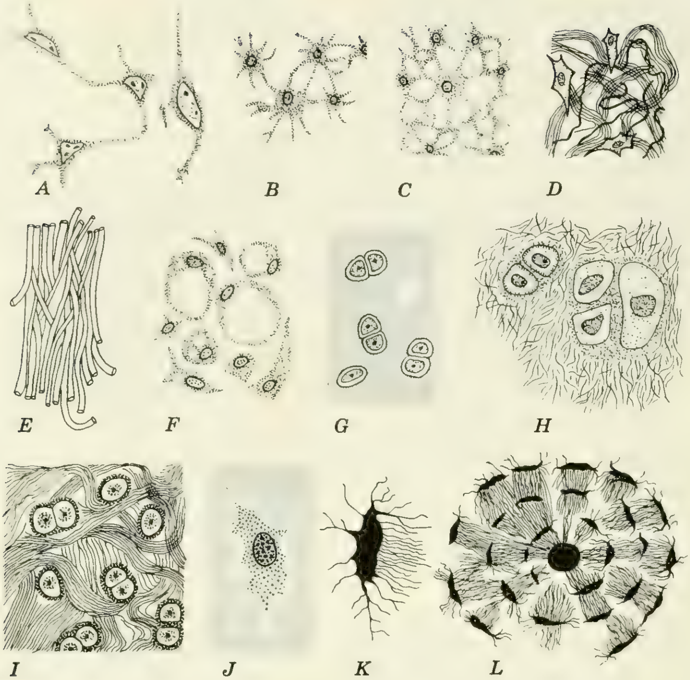


Fig. 3.15. Sustentative tissues. *A*, cells of mucous connective tissue, which occurs in the umbilical cords of mammals; the gelatinous intercellular material is not represented. *B*, mesenchyme cells. *C*, reticular connective tissue from the spleen. *D*, fibrous connective tissue from the submucosa, showing both collagenous and elastic fibers. *E*, elastic fibers of fibrous connective tissue from the nuchal ligament of the ox; no cells are shown. *F*, adipose tissue, showing various stages of storage of fat drops in the cells. *G*, hyaline cartilage from the end of a rib, showing cells and an empty lacuna. *H*, elastic cartilage from the external ear, showing capsules of hyaline cartilage and elastic fibers. *I*, fibrous cartilage from an intervertebral disk, showing capsules of hyaline cartilage and collagenous fibers. *J*, bone cell lying in a lacuna. *K*, bone lacuna and canaliculi from dried bone. *L*, Haversian system in which lacunae are arranged concentrically around a central or Haversian canal; canaliculi connect the lacunae and the canal. (*A*, *E*, *H*, *K*, and *L* from drawings by D. F. Robertson.)

between the vertebrae has collagenous fibers in its matrix and is called **fibrous cartilage** (Fig. 3.15*I*).

Bone, or osseous tissue, is characterized by its very hard matrix, which is impregnated with calcium and phosphorus salts. There is twice as much inorganic material in bone as there is organic. The long bones of the body, such as the femur, have a central marrow cavity filled with yellow or fatty bone marrow. In the much smaller marrow spaces at the ends of long bones and in the vertebrae and sternum is found the **red bone marrow,** which is the site of differentiation of red blood cells and of granular white blood cells. Bone marrow is not osseous tissue; it is merely contained in the cavities of bones. The bone cells lie in lacunae within the matrix (Fig. 3.15*J* and *K*).

A very typical arrangement is that of the **Haversian system**. This consists of a central Haversian canal which contains an artery, a vein, and a nerve, surrounded by concentrically arranged rows of lacunae in communication with one another and with the central canal by means of minute spaces, the **canaliculi** (Fig. 3.15*L*). Lymph circulates in these canaliculi and furnishes a passageway for foods and wastes between blood and cells.

In **adipose tissue** there is no intercellular material, and the stellate mesenchyme cells become transformed into rounded cells which serve to store fat (Fig. 3.15*F*). In fully differentiated adipose cells a large drop of fat is surrounded by a film of cytoplasm, which contains the nucleus. The large drop of fat is formed by the coalescence of numerous finer drops that are deposited in the cytoplasm during the specialization of fat-storing cells. Adipose tissue is widely distributed in the body.

Vascular Tissue. The vascular or circulating tissues are the blood and lymph and are characterized by a liquid intercellular material, the **plasma**. In **blood**, two kinds of cells are suspended in the plasma. Of these the **red blood cells**, or **erythrocytes**, contain the iron-bearing hemoglobin in combination with which oxygen is carried in the blood (Fig. 3.16*A* and *B*). The average human being has about 6 liters of blood, and each cubic millimeter of it contains 4½ to 5 million red blood cells. In mammals the red cells lose their nuclei during their differentiation, live only about 125 days, and must be replaced constantly. Red blood cells are differentiated in the red bone marrow in adults, and, if they are not formed in adequate numbers, the individual becomes anemic. The red cells are destroyed by macrophages located along the walls of the capillaries of the spleen and liver; 7 to 10 million red cells are destroyed every second.

White blood cells are frequently irregular in shape, since they are capable of amoeboid movement and migrate through the walls of capillaries and among the cells of other tissues (p. 54). Wandering white blood cells can

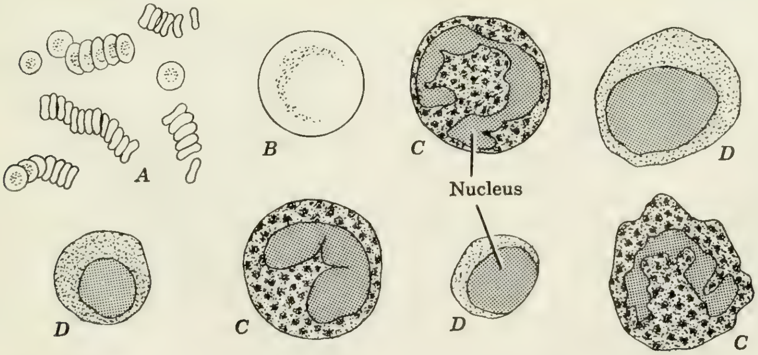


Fig. 3.16. Vascular tissue. *A*, mammalian erythrocytes arranged in rouleaux. *B*, single mammalian erythrocyte (non-nucleated). *C*, granular leucocytes with polymorphic nuclei; one with irregular cytosome. *D*, non-granular leucocytes or lymphocytes.

ingest solid particles like bacteria and other foreign bodies into their cytosomes and function in this way in the event of infections or wounds in any part of the body. These white blood cells are known as microphages. In connective tissue other white blood cells, the macrophages, are the chief local defenders in what is known as the inflammatory reaction, or first line of bodily defense, at the site of an infection. There are only about 8,000 to 10,000 leucocytes in a cubic millimeter of blood in a healthy individual, but the number may be greatly increased in illness. Enormous numbers of leucocytes are held in reserve in the bone marrow and can be quickly released to the blood stream in response to stimulation. Blood counts are effective aids in the diagnosis of disease. Two main classes of white blood cells are distinguished, those in which the cytoplasm does not contain granules and those in which the cytoplasm is granular. The most abundant kind of non-granular leucocyte is the **lymphocyte** (Fig. 3.16*D*), which is about the size of an erythrocyte and is differentiated in the lymph nodes and in the spleen. Another much less frequent and larger non-granular leucocyte is the **monocyte.** Granular leucocytes, all of which are larger than the other blood cells, have nuclei conspicuously irregular in shape and are called **polymorphonuclear leucocytes** (Fig. 3.16*C*). There are three kinds, distinguished by the staining reactions of the cytoplasmic granules. Granular leucocytes differentiate in the red bone marrow.

It has proved very difficult to obtain information concerning the life span of white blood cells. Lymphocytes apparently rupture or dissolve in great numbers soon after they leave their places of differentiation, contributing their globulins, a kind of protein, to the blood plasma. Gamma globulin is concerned in the formation of antibodies against certain diseases. In cats and dogs it appears that the total population of white blood cells is replaced several times a day.

Slightly more than half the volume of the blood is normally plasma, which is the carrier for all substances, except the oxygen, transported by the blood. Plasma contains, in addition to the blood cells, the blood **platelets,** which appear to be fragments of cytoplasm of uncertain origin and function. It also contains many submicroscopic constituents which are very important. One of these is a protein known as **fibrinogen;** when blood clots, this becomes changed to **fibrin,** in the meshes of which the cells are held. The clotting of blood acts to seal damaged blood vessels and prevent further loss of blood. Blood does not clot unless a vessel is ruptured, except when there has been tissue damage. In circulating blood there is a substance known as **prothrombin,** the formation of which depends on the presence of vitamin K (p. 32). In the presence of calcium salts, prothrombin is transformed into **thrombin,** which, in turn, conditions the change of fibrinogen to fibrin. This reaction does not occur in a closed blood vessel because of a substance called **heparin,** or **antithrombin.** When a vessel is broken, the damaged tissue cells and also disintegrating platelets release a substance known as **thromboplastin,** or **thrombokinase,** which neutralizes the effect of heparin. Then thrombin is formed from prothrombin, and, in turn, fibrin is formed from fibrinogen; a clot occurs. When drawn blood clots in a bowl and is allowed to stand, the clot contracts, and a pale yellowish fluid is squeezed out. This fluid is what remains of the original plasma. It is called blood **serum** and contains, among other things, the substances which immunize against certain diseases.

One very important function of the blood is the transport of oxygen in combination with the hemoglobin of the red blood cells. Death results from loss of one-third the blood in warm-blooded animals because oxygen is no longer delivered to the cells of the body in adequate amounts. In medical practice a blood transfusion may save a life after hemorrhage or in severe anemia. When transfusion was first attempted, it was often found that the patient died as soon as blood from another person was introduced into his vessels. The reason was that the red cells of the donor blood clumped or stuck together; they were agglutinated as a result of a reaction between proteins of the plasma and proteins of the red cells. These clumps prevented the free flow of blood in the capillaries and thus caused death. About 1900 it was discovered that the blood of any human being falls into one of four types, depending on the presence in the red cells of either substance A or B, of both A and B (AB), or of neither A nor B (O). About 46 per cent of the human race have blood of type O; 42 per cent, type A; 9 per cent, type B; and 3 per cent, type AB.

The substances A and B are examples of what are called **antigens.** The substances in the plasma which react with A and B to bring about agglutination are examples of **antibodies.** These are what are known as normal antigens and antibodies. In an individual with type A blood the red cells contain antigen A and the antibody for A does not occur in the plasma. Such individuals carry antibodies for antigen B. If blood of type B or type O is placed in the vessels of a type A individual agglutination can occur because antibodies for A are present in the plasma of type B and type O blood. In emergencies it is sometimes possible to use type O blood to transfuse a type A or type B individual depending on the amount of blood required and the concentration of antibodies A or B in its plasma.

Proteins, such as those of bacteria, which are foreign to a certain kind of animal and which invade its tissues are also known as antigens. The tissues of the animal react to the presence of the foreign protein by producing antibodies that combat the effects of the antigen. Such antibodies are called immune antibodies and become abundant in the blood plasma, where they remain for varying lengths of time and provide immunity to reinvasion by the foreign protein or antigen that conditioned their production. Thus, recovery from a particular disease may result in permanent or transitory **active acquired immunity** to that disease.

The capacity of animals to synthesize substances protective against foreign proteins can be utilized to protect human beings against diseases. If minute quantities of the pathogenic material are introduced into the body, its tissues will produce abundant antibodies, even though the amount of infective material gives only transitory symptoms of the disease. Thereafter, these antibodies are responsible for an **artificial acquired immunity** to the disease in question; this immunity may be permanent or may have to be renewed at intervals. Dead bacteria are used for inoculation against typhoid and paratyphoid; viruses of reduced virulence, called attenuated viruses, are used in vaccination against smallpox or inoculation against rabies. The toxins, or poisonous substances, produced by the bacteria are injected in inoculation against diphtheria.

Antibodies produced in other animals can be used to give **passive immunity,** usually of short duration, or to combat antigens in human beings in the control of disease. Thus, antibodies, also called antitoxins, against the toxin giving symptoms of diphtheria are produced by horses inoculated with the toxins of the diphtheria bacilli and can be obtained in the serum which separates when the horse's blood clots after being drawn. Such **immune serum** administered to an individual enables him to combat effectively the toxin or poison of the diphtheria bacillus before antibodies are produced in adequate quantities in his own tissues. After a wound is received under circumstances where tetanus bacilli might be present, tetanus antitoxin, also from horses, is routinely administered, in order to protect against the toxins these bacilli would produce. Soldiers in World War II were given inoculations of tetanus toxin and antitoxin in order that they might acquire artificial immunity against this rapidly fatal bacterium.

It may be noted here that some individuals have what is called **natural immunity** to certain diseases. This immunity may be the result of inheritance of a capacity to form certain antibodies, such as the natural antibodies against antigens A and B of the red blood cells. Very slight and unnoticed infection with the causal agent of the disease may also bring about what seems to be natural immunity.

Immunity and resistance to disease must not be confused. Immunity is protection against a specific pathogenic agent. Resistance is non-specific and may depend on many factors.

The quantity of blood in the circulatory system is important in connection with the ease of its circulation and the adequacy of supply to all regions. When blood is lost in amounts insufficient to cause death from oxygen want, a condition known as shock may result. This condition can be controlled by increasing the blood volume through the addition of plasma without the red cells. Typing is not necessary for such transfusions. In World War II one of the greatest contributions of science to the saving of human life was the development of methods of separating the plasma from the great quantities of blood donated by non-combatants, preventing it from clotting, and drying it in such a way that it would keep indefinitely. The dried powder was sent to all fronts along with triple-distilled water, with which it was mixed before use in combating shock in wounded men.

Lymph differs from blood in that it does not contain erythrocytes and granular leucocytes. The plasma of lymph is derived from the blood by filtration through the walls of the capillaries and does not contain all the constituents of blood plasma. Lymph is important as the pathway over which pass the materials transferred between blood and the cells of the body.

Contractile Tissue. Contractile tissues, made up of what are known as muscle cells, are of three kinds: non-striated, cardiac, and striated. The cytoplasm of muscle cells is characterized by the presence of numerous fine fibers, which are placed longitudinally. The shortening and thickening of these **muscle fibrillae** result in the contraction of the individual cell and are therefore responsible for the particular function of this kind of tissue, the production of motion. **Non-striated muscle** cells are typically spindle-shaped with the nucleus centrally placed (Fig. 3.17*A* and *B*). These cells usually occur in sheets loosely held together by fibrous connective tissue. This kind of muscle is found in the wall of the digestive tract, in the urinary bladder, and in the walls of blood vessels. It is sometimes called involuntary muscle because it is not under conscious nervous control.

Cardiac muscle is found only in the heart and is capable of rhythmical contractions (Fig. 3.17*F*). The cells are arranged in the form of a syncytium; that is, the cylindrical cytoplasmic units containing the nuclei are not separated from one another by membranes where they meet at their ends.

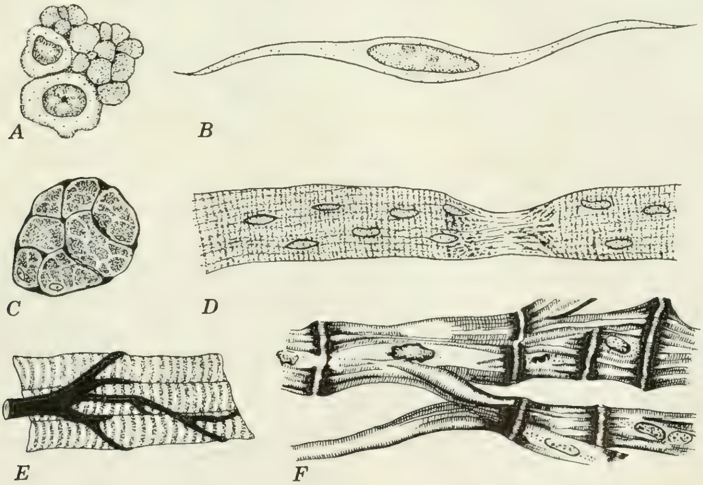


Fig. 3.17. Contractile tissues. *A*, non-striated muscle cells in cross section; note that the cytosomes of many of the cells are not cut through in the region of the nucleus. *B*, isolated non-striated muscle cell from the wall of the digestive tract, showing spindle-shaped cytosome and single nucleus. *C*, cross section of a voluntary muscle; the striated muscle cells are held together in bundles by fibrous connective tissue. *D*, portion of a striated muscle cell, showing its multinucleate condition and the cross-striations; the cell has been injured near its right end in order to show the cell membrane. *E*, striated muscle cells, showing blood supply. *F*, cardiac muscle cells from the human heart. (*A*, *B*, *C*, and *E* from drawings by D. F. Robertson; *F*, from E. A. S. Schäfer, *Essentials of Histology*, copyright 1916 by Longmans, Green and Co., reprinted by permission.)

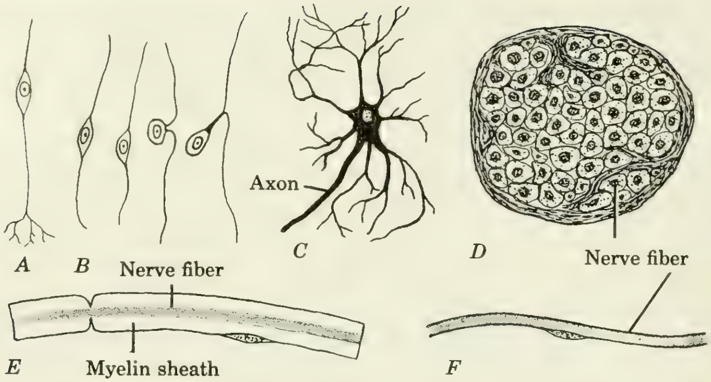


Fig. 3.18. Nervous tissue. *A*, typical bipolar neuron from the olfactory epithelium. *B*, transformation of a bipolar neuron into the type found in the dorsal root ganglia of spinal nerves. *C*, multipolar neuron, showing cytosome with numerous dendrites and a single axon. *D*, bundle of myelinated nerve fibers surrounded by fibrous connective tissue, as in the spinal and cranial nerves; each nerve fiber is surrounded by a myelin sheath. *E*, portion of a single myelinated nerve fiber; the interruption in the myelin sheath is called a node of Ranvier; a nucleus is seen in the neurilemma, or outer membrane. *F*, portion of an unmyelinated nerve fiber, characteristic of autonomic nerves; a nucleus of the neurilemma is shown.

These units branch and unite in such a way that a network is formed. The fibrillae of cardiac muscle are made up of regions of different density so that the cytoplasm presents an irregularly striated appearance.

Striated muscle is known sometimes as skeletal muscle because it is attached to the bones and by its contractions produces motion of body parts which are supported by bones (Fig. 3.17*D* and *E*). Since these muscles can be coordinated consciously, they are also called voluntary muscles. They appear striated because the fibrillae have regions of different density, which occur at such regular intervals as to give a distinct cross-striped appearance to the cytoplasm. The cells are cylindrical, sometimes very long, and each contains many nuclei; that is, the cells are multinucleate. Fibrous connective tissue serves to bind together striated muscle cells and forms sheaths that enclose great numbers of these cells which make up the visible muscles, such as the gastrocnemius or the biceps (Fig. 3.17*C*). These connective tissue sheaths are continuous with the tendons by means of which muscles are attached to bones.

Nervous Tissue. The cells of nervous tissue are differentiated in such a way that they are capable of receiving stimuli in some regions, of conducting nerve impulses from one part of the body to another, and of discharging these impulses. The general functions of nervous tissue can, therefore, be stated as reception, conduction, and discharge. These activities make possible the coordination of the organism as a whole and will be discussed in the next chapter. A nerve cell, or **neuron**, is composed of a nucleus surrounded by a relatively small cytosome, which is prolonged into two or more processes of varying lengths; these **nerve fibers** are of two types. Some taper along their lengths and have branches which come off at varying angles; these are called **dendrites.** Others are seen to be of uniform, small diameter, with branches at right angles to the main fiber, and are surrounded by a myelin sheath containing compound lipids (Fig. 3.18*E*); these are the **axons.** Nerve fibers branch repeatedly at their ends, forming the terminal filaments. The terminal filaments of axons, which often end in plate-like or club-like expansions, lie against the dendrites and cell bodies of other neurons or on muscle and gland cells (see Fig. 4.22, p. 114). Where there are only two cytoplasmic extensions, or nerve fibers, the cell is called a **bipolar neuron** (Fig. 3.18*A* and *B*). Cells with more than two fibers are known as **multipolar neurons** (Fig. 3.18*C*). Such cells never have more than one axon. The cell bodies of neurons are sometimes found in groups, or **ganglia,** outside the central nervous system; other nerve cell bodies occur in the gray matter of the central nervous system (see Fig. 4.9, p. 96). When nerve fibers are bound together and surrounded by fibrous connective tissue, they form the visible **nerves** of the peripheral nervous system (Fig. 3.18*D*); nerve fibers also make up the white matter of the central nervous system. A nerve fiber is always continuous with the cytosome of a neuron.

Organs. The tissues that have been described illustrate the various types of specialization that cells undergo in the vertebrate body. Particular tissues are capable of performing their special functions alone, but they usually occur grouped in organs. Thus, **organs** are groups of tissues associated for the performance of a special function. For example, if the wall of the small intestine of a mammal or other vertebrate is examined microscopically, it is found to consist of layers known as the **peritoneum,** the **longitudinal** and **circular muscle layers,** the **submucosa,** and the **mucous membrane** (Fig. 3.19). The peritoneum

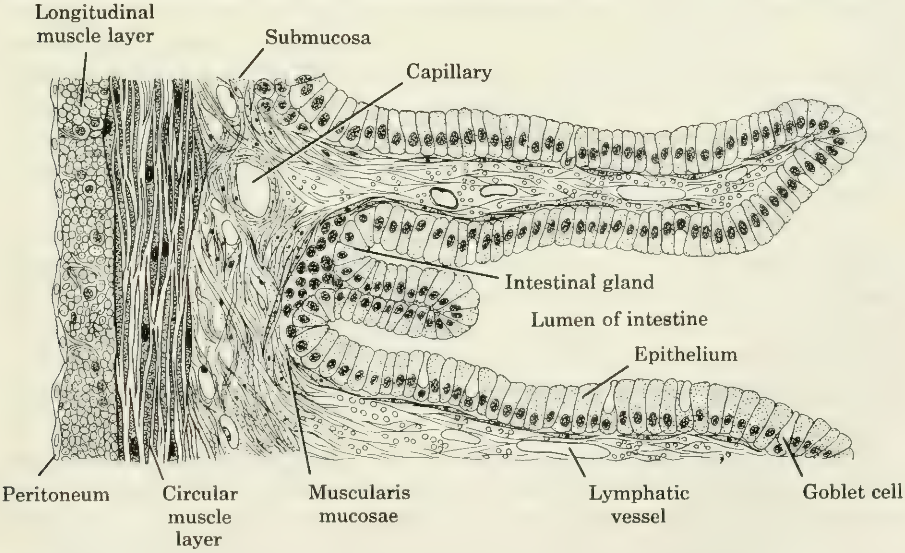


Fig. 3.19. The wall of the small intestine of an amphibian, in section; semidiagrammatic.

consists of simple squamous epithelium and functions as a covering membrane. Both longitudinal and circular muscle layers are of non-striated contractile tissue bound together by fibrous connective tissue, and their contractions produce the muscular movements that mix the food contents of the small intestine and push them along toward the large intestine. Fibrous connective tissue, containing both collagenous and elastic fibers, is the distinguishing tissue of the submucosa and serves to support the numerous vessels carrying blood and lymph. This layer also provides the elasticity essential for the expansion of the intestinal lumen, in addition to carrying the circulatory fluids necessary for absorption. The mucous membrane, functioning in secretion and absorption, is composed of simple columnar epithelium, which forms the lining of the tract; a layer of reticular connective tissue (lamina propria), which forms the cores of the villi; and a thin layer of non-striated muscle cells (muscularis mucosae), which is the outermost layer lying adjacent to the submucosa. These several tissues are associated to form the small intestine, in which digestion and absorption occur, and each tissue contributes to the function of the whole organ. In addition to the grouping of cells to form tissues and of tissues to form organs, organs are associated to form the systems described in discussions of metabolism, responsiveness, and reproduction.

Digestion

Most of the food that a vertebrate eats, or ingests, is not in a form immediately utilizable by its cells. Foods, with the exception of water, inorganic salts, vitamins, and a very few lipids and monosaccharides, must be broken down into smaller units before they can be absorbed and utilized by the animal. The processes of chemical breakdown of foods during their passage through the digestive tract are called **digestion**. The chemical changes in the food are brought about by specific enzymes secreted by cells of the digestive organs. As a result of enzyme action, carbohydrates are broken down into hexose sugars, lipids are separated into fatty acids and glycerol, and proteins are reduced to amino acids.

The purely mechanical activities of the digestive tract are aids to digestion. Chewing separates food into smaller masses which afford more surface area for the action of digestive enzymes. Movements of the digestive tract mix the food particles with digestive juices and propel the food mass from one region of the tract to the next. Digestion will be discussed as it occurs in the successive regions of the digestive tract. You should keep in mind the structure of the digestive system (p. 47).

In the mouths of mammals the food may be torn apart or ground into fine particles by the teeth, but in many other vertebrates the food is merely held by the teeth and no mechanical disintegration occurs. The frog, for instance, retains food with its teeth until it can be swallowed, and no digestive changes take place in the mouth. In man, however, the sight, the odor, or even the thought of food induces the flow of **saliva**, a digestive juice secreted by the salivary glands; the average daily output is about 1500 ml. As the food is chewed, it is mixed with saliva which softens and lubricates the food. This initiates the digestive changes and aids in swallowing. Although saliva is largely water and mucin, it contains a digestive enzyme, a salivary amylase known as **ptyalin**. This enzyme is most active in a neutral medium and is responsible for the partial digestion of glycogen and starch. Starch, if it has been cooked, enters the mouth in soluble form; if not, it is made soluble by the ptyalin. Soluble starch in the presence of ptyalin reacts with water to form dextrins and maltose, one of the compound sugars. The food mass, with its complex carbohydrates partially digested, is carried down the esophagus by the muscular movements known as swallowing. No digestive changes occur in the esophagus; it is merely a passageway.

Once the food mass is in the stomach, salivary digestion may continue for 15 to 20 minutes until the acid of the stomach penetrates the mass. Digestion of carbohydrate is resumed in the small intestine.

Food is retained in the cavity of the stomach because of the contraction of the pyloric sphincter. Muscular movements of the stomach wall thoroughly mix the mass with the digestive juice of the stomach which is known as **gastric juice**. This juice, secreted by the gastric glands of the stomach lining, is strongly acidic because of the presence of hydrochloric acid. It contains **pepsin**, an enzyme responsible for most of the digestive activity in the stomach. Pepsin is secreted by the gland cells in an inactive form known as pepsinogen. In the presence of hydrochloric acid, pepsinogen is converted to pepsin. For its effective action this enzyme requires a strongly acid medium which is normally present in the stomach. Pepsin breaks certain of the peptide linkages of proteins, producing fragments of considerable size called proteoses and peptones.

In the stomachs of young milk-feeding animals, including the human infant, another enzyme, called **rennin**, is found in the gastric juice. The action of this enzyme is to clot casein, the protein of milk, forming paracasein. Paracasein combines with calcium to form an insoluble compound which remains in the stomach for some time, permitting more prolonged digestion by pepsin. Rennin does not occur in the gastric juice of adults.

Degradation of proteins does not go to completion in the stomach. Once the food is liquefied it is pushed through the pyloric sphincter, without regard for the degree of protein digestion, into the small intestine.

The muscular activities of the small intestine are of two types, known as peristalsis and segmentation. In **peristalsis** a muscular contraction begins at the upper end of the intestine and passes with wave-like effect toward the lower end. This motion has a tendency to bring about the movement of the food mass toward the large intestine. **Segmentation**, on the other hand, consists of a series of contractions occurring close together and simultaneously at different levels of the intestine. This results in a pinching of the food mass into segments; and, since these segmentation contractions disappear and reappear at alternate levels, they produce a very thorough mixing of the intestinal contents.

Food in the small intestine is acted upon by three digestive juices: **bile,** secreted by the liver and stored in the gall bladder, enters the intestine by way of the bile duct; **pancreatic juice,** secreted by the pancreatic acini (see Fig. 4.25, p. 120), comes from the pancreas through the pancreatic duct; and **intestinal juice** comes from intestinal glands in the lining of the duodenal portion of the small intestine. It is well to realize that food entering the small intestine is exposed to the simultaneous action of the various enzymes of these juices, all maximally effective in the alkaline medium of this region. Thus, digestion is a continuous process, not so neatly subdivided as our discussion may suggest.

Bile, although it does not contain any digestive enzymes, is an important aid to digestion and absorption. It serves chiefly as an emulsifying agent for lipids, which in its presence become divided into very fine droplets; these offer a large surface for the action of the fat-splitting enzyme. In addition, bile stimulates motility of the intestine and is an effective neutralizer of the acid food mass coming from the stomach.

Pancreatic juice, which is also strongly alkaline, contains three types of digestive enzymes, acting on proteins, carbohydrates, and lipids, respectively. Because of its wide spectrum of action, pancreatic juice is by far the most important single digestive juice. In man approximately 750 ml. is secreted each day. Several enzymes in pancreatic juice act on proteins. Of these, the proteinases **trypsin** and **chymotrypsin** reduce protein, or proteoses and peptones resulting from prior pepsin digestion, to smaller fragments known as polypeptides. Chymotrypsin also clots milk and renders its digestion more effective. Both trypsin and chymotrypsin are secreted in the form of inactive precursors known, respectively, as trypsinogen and chymotrypsinogen. These are converted to the active enzymes in the small intestine. Another protein-splitting enzyme, the peptidase called **carboxypeptidase,** acts on certain polypeptide linkages, freeing some of the amino acids. The most effective splitter of the complex carbohydrates, **pancreatic amylase** or amylopsin, is present in pancreatic juice. It changes starch, glycogen, or the dextrins formed during the action of salivary amylase to maltose, a disaccharide. Finally, a **pancreatic lipase,** sometimes called steapsin, is found in pancreatic juice. This enzyme is an effective splitter of emulsified lipid into fatty acids and glycerol.

Intestinal juice is not such a well-defined entity as the other digestive juices. It is known to contain certain peptidases, specifically **aminopeptidase** and **dipeptidase,** which act on polypeptide fragments and reduce them to amino acids. Also, there are several enzymes which complete the digestion of carbohydrates. These are disaccharidases, specifically **maltase, sucrase,** and **lactase** which split the disaccharides, yielding monosaccharides or simple sugars.

The final stages of digestion of all foods occur in the small intestine. Digestion is normally so efficient that there is very little usable food discharged into

Regions of Digestive Tract	Digestive Juices and Optimum *p*H Conditions	Sources of Digestive Juices	Digestive Enzymes		Foods Changed	End Products
			Type	Name		
Mouth cavity	Saliva (neutral)	Salivary glands	Amylase	Ptyalin	Carbohydrates (starch, glycogen)	Dextrins and maltose
Esophagus	None	None	None		None	None
Stomach	Gastric juice (acid)	Gastric glands	Proteinases	Pepsin	Proteins	Proteoses and peptones
				Rennin (not present in adults)	Milk protein coagulated, combined with calcium	Calcium paracaseinate
Small intestine	Bile (alkaline)	Liver	None		Lipids emulsified	
	Pancreatic juice (alkaline)	Pancreas	Amylase	Amylopsin	Carbohydrates (starch, glycogen, dextrins)	Maltose
			Proteinases	Trypsin	Proteins, proteoses, and peptones (chymotrypsin also coagulates milk protein)	Polypeptides
				Chymotrypsin		
			Peptidase	Carboxypeptidase	Polypeptides	Amino acids
			Lipase		Lipids (emulsified)	Glycerol and fatty acids
	Intestinal juice (alkaline)	Intestinal glands	Peptidases	Aminopeptidase	Polypeptides	Amino acids
				Dipeptidase		
			Disaccharidases	Maltase	Disaccharides: Maltose	Monosaccharides: Glucose
				Lactase	Lactose	Glucose and galactose
				Sucrase	Sucrose	Glucose and fructose
Large intestine	None	None	None		None	None

Fig. 3.20. The principal facts about digestion.

the large intestine through the ileocaecal valve. In man the first part of the food mass enters the large intestine about 4 hours after having been eaten, and the discharge continues for about 2 hours. After being retained in the lower part of the large intestine for from 10 hours to 2 days, this undigested and undigestible material, now known as feces, is egested or defecated. The amount of material egested is about 10 per cent of the amount ingested. In the large intestine of herbivorous animals there are many bacteria which digest cellulose, a carbohydrate present in the walls of plant cells, and produce simple sugars from it. Although some of this sugar is absorbed, it must be kept in mind that the bacteria digest this material for their own use. It is only incidentally that it affords nourishment for the animal harboring the bacteria. Bacteria in the digestive tract of many animals produce substances important for their hosts' growth and maintenance. For example, in man intestinal bacteria produce vitamin K (p. 32) and vitamin B_{12} (p. 34). Some idea of the great number of bacteria comprising the intestinal flora can be had when it is stated that from one-fourth to one-half the dry weight of feces consists of bacteria.

The principal facts about digestion are summarized in Figure 3.20, which should be carefully studied in tracing the breakdown of each of the classes of foods as they pass along the digestive tract.

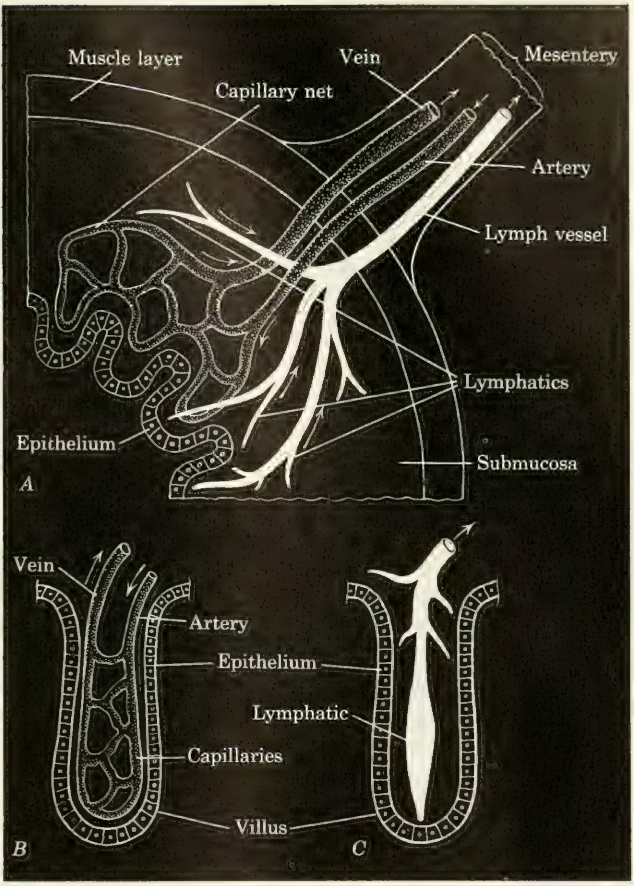
Absorption

The simple nutrients which are the end products of digestion must be absorbed from the digestive tract into the circulating fluids and be distributed to all the cells of the body before they can take part in cellular metabolism. **Absorption** may be defined as the passage of simple food compounds through the cells lining the digestive tract into the blood or lymph. Between the mucous membrane and the muscular coats of the tract is the submucosa, a region of loosely arranged cells with interlacing fibers (Fig. 3.19). It is in this region, separated from the digestive cavity by the mucous membrane, that the delicate lymphatics and the thin-walled capillaries which connect arteries and veins are found (Fig. 3.21). In being absorbed, substances pass through the cells of the mucous membrane and endothelium of the capillaries, as well as the small amount of lymph between the two.

Two mechanisms are responsible for the phenomenon of absorption—**diffusion**, or movement from a region of high concentration (lumen of intestine) to a region of lower concentration (epithelial cell of intestinal lining), and **active transport**. Diffusion obeys certain physicochemical laws in the living organism as in non-living systems. Active transport requires expenditure of cellular energy to move substances from the lumen of the intestine into the intestinal epithelium.

Although certain foods, such as glucose, vitamins, water, and the inorganic salts, require no change before they are ready for absorption, they are not

Fig. 3.21. Blood and lymph vessels in the wall of the digestive tract; diagrammatic. *A*, a portion of the entire wall. *B*, capillaries in a villus, or finger-like projection of the wall of the intestine. *C*, lymphatic in a villus of the intestine. Arrows indicate direction of movement of blood and lymph.



absorbed from the stomach. Only alcohol is freely absorbed from the stomach. The small intestine is the chief organ of absorption. In the upper part of the small intestine the surface of the mucous membrane is greatly increased by folding and, in mammals, by the projection of numerous finger-like villi. In man it has been estimated that there are 5 million villi and 10 square meters of absorptive surface. Amino acids and inorganic salts pass through the epithelial lining directly into the blood stream as a result of diffusion. Glucose, on the other hand, must first be converted at the cell surface into glucose phosphate. This phosphorylation under the direction of a specific enzyme requires energy supplied by ATP. The glucose phosphate is rapidly absorbed by the epithelial cells, and glucose soon appears in the blood stream.

Lipids are often not completely broken down to fatty acids and glycerol. However, under the emulsifying effect of the bile salts, lipid is dispersed into minute droplets, 0.5 micron or less in diameter. These very fine droplets of lipid enter the epithelial cells and pass directly into the lymphatics of the

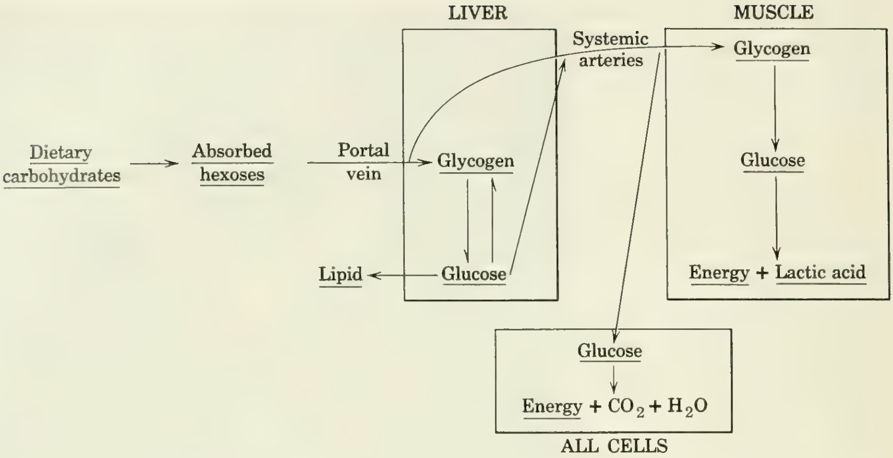


Fig. 3.22. Transport, storage, and use of carbohydrates.

submucosa; the mechanism of their movement remains to be discovered. About a third of the dietary lipid is completely digested to form fatty acids and glycerol. Glycerol is absorbed by diffusion and enters the blood stream. The fatty acids form a complex with certain bile salts. This complex is soluble and passes by diffusion into the epithelial cells. There it is freed from the bile salt and converted by synthetic metabolism into a phospholipid; this lipid then passes into the blood stream. Absorption of the fat soluble vitamins, A, D, and K, is also dependent on the presence of bile salts. In the absence of bile, deficiency of these vitamins may occur (p. 31)

The large intestine is the chief site of water absorption. Pyridoxin, folic acid, and vitamin B_{12} (p. 34), which are synthesized by the bacteria of the large intestine, are also absorbed there.

Transport and Storage of Food

Animals eat at intervals, as food is available. The products of the intermittent meals are handled in such a way as to provide for the continuous metabolic requirements of the cells of the body. This involves the maintenance of suitable levels of nutrients in the blood at all times. In the case of carbohydrates and lipids, the organism stores some of the abundant supplies available after eating; later these can be returned to the blood to satisfy metabolic demands. It is relatively easy to determine the general pattern of movement, storage, and reconversion of the absorbed carbohydrate and lipid. In the case of the amino acids, it was not until it became possible to tag them with radioactive isotopes of carbon and nitrogen that we became aware of their almost ceaseless journeys in the body.

The monosaccharides glucose, fructose, and galactose are absorbed into the blood in the capillaries of the wall of the small intestine and carried by way of the hepatic portal vein to the capillaries of the liver (Fig. 3.22). Here, under normal conditions, a considerable amount passes into the cells of the liver where it is converted to the complex carbohydrate glycogen for storage. Leaving the liver, the blood still contains more than the normal level of simple sugar. In muscle cells more of it is converted to glycogen, and the blood sugar level soon returns to its normal range of 70 130 mg. per 100 ml. Everywhere in the body as the blood passes through capillaries, glucose enters cells and undergoes the metabolic changes discussed previously (p. 35). The level of blood sugar is maintained between meals as a result of the conversion of liver glycogen to glucose which re-enters the blood. Muscle glycogen is utilized during muscle contraction and does not contribute to the blood-sugar level. The human body contains about 200 grams of glycogen, equally distributed between the liver and muscles. Radioactive labeling of glucose reveals that a considerable amount is converted to fat and stored as such.

Much of the lipid is absorbed into the lymphatic vessels in the wall of the intestine and, in man, is carried to the left subclavian vein by way of the thoracic duct (Fig. 3.23). A sample of blood plasma taken a few hours after a meal rich in fat has been eaten appears milky because of the large number of suspended fat droplets. This fat is promptly stored in the fat depots of the body, such as the subcutaneous and intramuscular connective tissue and the mesenteries of the peritoneal cavity. Stored fat is a readily available source of fuel for the cells. In other words, fat does not go into dead storage; the depots are very labile. It should be noted that stored fat has important insulating properties in connection with the conservation of heat and main-

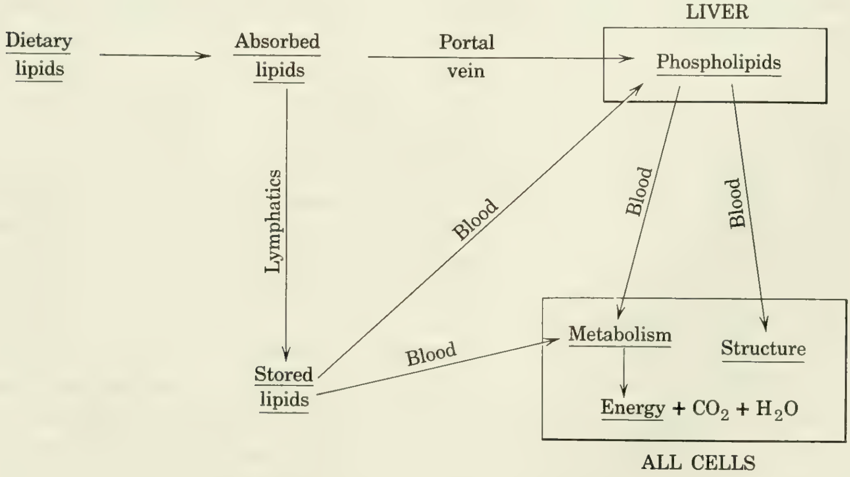


Fig. 3.23. Transport, storage, and use of lipids.

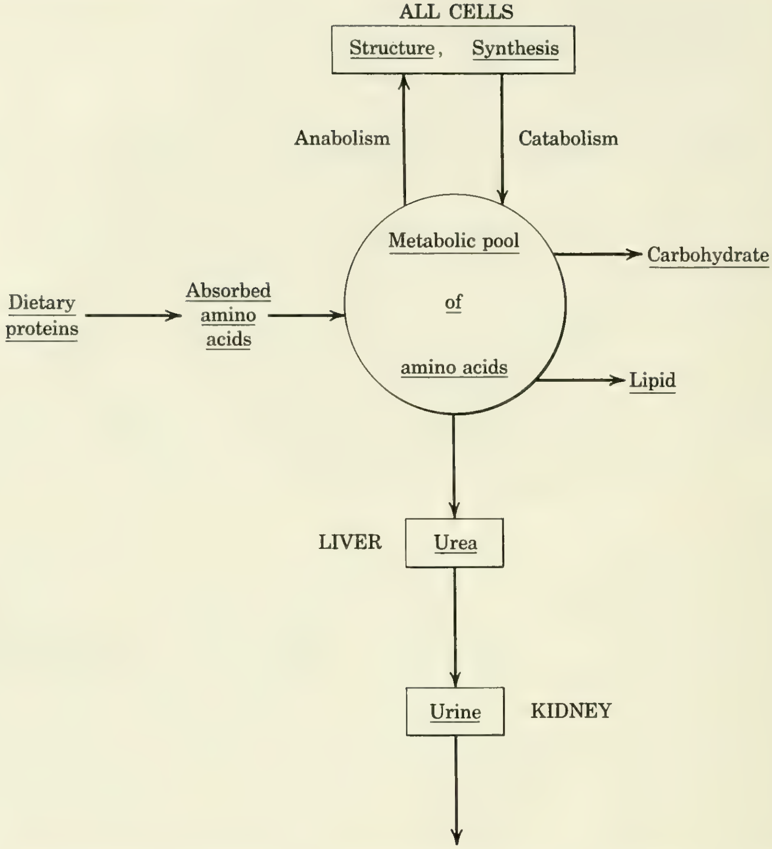

ALL CELLS
Structure, Synthesis
Anabolism
Catabolism
Metabolic pool of amino acids
Carbohydrate
Lipid
Dietary proteins
Absorbed amino acids
LIVER
Urea
Urine
KIDNEY

Fig. 3.24. Schema showing dynamic quality of protein metabolism in mammals. In the continuous metabolic turnover, proteins from the diet or from any one tissue can contribute to the protein of any other tissue or be degraded.

tenance of body temperature. It also plays a protective role as filling or packing material about and between organs.

Some of the fatty acids and glycerol are absorbed into the blood and pass to the liver capillaries. The liver is not normally a fat depot. Instead, the important function of the liver in fat metabolism is the synthesis of phospholipids which are returned to the blood to be used by all cells. Glycerol can be converted to glucose.

Unlike the hexoses and lipids, the amino acids absorbed into the blood are not stored (Fig. 3.24). They are removed by all cells in connection with the synthesis of protein for maintenance and growth. Excess amino acids can be converted to glucose and then to fat and stored; this is an irreversible reaction. Amino acids can also be converted to glucose and be used as fuel for the cell. During their conversion to glucose the amino acids are deaminated; that is, they lose their $-NH_2$ or amine groups. The liver is the chief site of degradation of excess or worn-out amino acids. In mammals, urea, the chief nitrogenous waste product, is formed during this process. Birds and reptiles build the amine groups from the breakdown of amino acids into uric acid. In aquatic vertebrates, the amine groups become ammonia (NH_3). Studies with labeled amino acids reveal a constant state of flux or shifting of individual molecules between the so-called structureless pool and the formed proteins throughout the body.

Respiration

The term respiration has been widely used to cover the so-called gaseous metabolism of the organism. In the discussion of cellular metabolism (p. 35), it was shown that oxygen was required for the final steps in the complete extraction of energy from the organic foods. The oxidative reactions release carbon dioxide, which is a gaseous waste product and must be removed if cellular metabolism is to continue normally. In unicellular organisms, oxygen enters the cell as a result of diffusion gradients between the contents of the cell and its surroundings. In multicellular organisms and especially in the complex vertebrate, a well-defined respiratory system functions, together with the circulatory system, to satisfy the gaseous requirements for cellular metabolism.

The discussion of respiration in terrestrial vertebrates will be broken down into three distinct, though continuous, phases. The first of these is **pulmonary respiration,** or external respiration as it is sometimes called. This is subdivided into **ventilation,** the movement of the air mass in and out of the lungs, and **gas exchange,** the simultaneous diffusion of oxygen and carbon dioxide between the alveoli of the lungs and the blood stream. The second aspect of respiration to be discussed is the **circulatory phase.** This includes **gas transport** between the lungs and cells in all parts of the body and **gas exchange** between the blood and these cells. The third phase of respiration is **cellular respiration** or **biological oxidation,** which has been discussed previously (p. 37).

Air usually contains about 20 per cent oxygen, 0.04 per cent carbon dioxide, and 79 per cent nitrogen. Terrestrial vertebrates live at the bottom of a sea of air, and just as in the ocean the pressure is greatest at the bottom. At sea level, the air we breathe has a pressure of 14.7 pounds per square inch. This is usually indicated by stating that the air pressure will support a column of mercury 760 mm. high. Animals must breathe air under pressure in order to live. At high altitudes, the atmospheric pressure decreases although the actual gas content varies little. At altitudes greater than 18,000 feet, where the atmospheric pressure is only 380 mm. of mercury, oxygenation will be inadequate unless corrective measures are taken. At 50,000 feet, man loses consciousness in about 14 seconds and will die unless pure oxygen is immediately supplied under pressure. There is so little pressure at 63,000 feet that the blood will actually seem to boil. The reduced atmospheric pressure at high altitudes makes it difficult or even impossible for men to breathe. Consequently, adequate air pressure must be artificially maintained in aircraft operating at high altitudes, and above 48,000 feet pilots are obliged to wear pressurized suits. With advances in physiology, as well as in aviation and space technology, new altitude records are constantly being set. At 126,000 feet, an altitude reached some time ago, 99.6 per cent of the atmospheric mass lies below. Living creatures sent into space in rockets have returned alive; mice, dogs, monkeys, and even men have now traveled successfully in space, beyond the limits of our atmosphere, in properly equipped, pressurized capsules. A thorough understanding of the physiology of respiration and associated circulatory functions in the normal individual, together with experimentation to achieve safeguards for these bodily requirements, is a necessary prerequisite to man's conquest of outer space.

Ventilation of the lungs requires muscular work. As the muscles of the chest, or thoracic cage, contract, air moves from the external environment into the air passages and lungs. In a 24-hour period of normal muscular activity, something like 10,000 liters of air are moved into the lungs of man, about 500 ml. at each inhalation. The same volume is, of course, exhaled when the respiratory muscles relax and the inherent elasticity of the thoracic structures snaps the lungs back to their collapsed capacity. When it is necessary, or if an individual desires, a much greater volume of air can be moved as a result of more vigorous muscular contractions which not only pull air into but, also, actively force it out of the lungs. Under these conditions, the volume of air inhaled may amount to 4500 ml. for a single maximal muscular effort, depending on the age and size of the individual. In an adult man, about 1 liter of air always remains in the lungs in spite of maximal effort to blow out all the air. This is important because it means that any fresh air pulled into the lungs is mixed with and diluted by the partly used air that cannot be expelled. Therefore, air in the alveoli of the lungs where gas exchange occurs contains only about 15 per cent of oxygen instead of the 20 per cent present in the outside air, and 5.6 per cent of carbon dioxide instead of 0.04 per cent.

A survey of the multicellular animals reveals that many different structures have been evolved to capture oxygen from the atmosphere for eventual use in cellular oxidation. All have a common feature—the medium containing oxygen, be it water or air, comes in close approximation, through a very thin membrane, with blood or other body fluid. In man, this membrane is the epithelium lining the alveoli of the lungs. It has a surface area of nearly 1000 square feet, about 50 times that of the skin of the body. The respiratory membrane of man is composed of the alveolar membrane and the endothelium of the blood capillary; it is about 4 microns thick (Fig. 3.10).

Free gases in a mixture exert a tension or pressure in proportion to their concentration. If a membrane separates two mixtures of oxygen which exert different partial pressures because the concentration is different, oxygen will move from the region of higher pressure to the region of lower pressure until the pressure exerted by oxygen is equal on both sides of the membrane. This is what happens during gas exchange in the lung. Oxygen in the alveolar air exerts a partial pressure of about 103 mm. of mercury. Blood entering the lung capillaries has a low concentration of oxygen exerting a partial pressure of only about 35 mm. of mercury. Consequently, oxygen diffuses across the respiratory membrane into the blood stream. The time required for the blood to pass through the capillary bed of the lung allows for almost complete equilibration of oxygen.

This same mechanism results in the elimination of excess carbon dioxide from the blood as it circulates through the capillaries of the lungs. During its course throughout the body, the blood has picked up the carbon dioxide formed during cellular oxidation. The partial pressure of carbon dioxide in blood entering the lung capillaries is about 46 mm. of mercury as compared with a partial pressure of 38 mm. of mercury exerted by the carbon dioxide in the alveolar air. Therefore, carbon dioxide diffuses from the blood into the alveolar air, and blood leaving the lung capillaries has a carbon dioxide pressure of 38 mm. of mercury.

Pulmonary gas exchange thus occurs as a result of diffusion. Blood leaving the lungs carries oxygen and carbon dioxide in concentrations equal to those in the alveolar air. The first hurdle in meeting the oxygen requirements of cells far removed from the external supply of oxygen has been cleared. Elimination of carbon dioxide through the lungs is, likewise, very important in bodily maintenance. Apart from the obvious necessity of getting rid of a waste product of cellular oxidation, the elimination of carbon dioxide helps to maintain the normal acid-base equilibrium of the body. The amount of carbon dioxide eliminated each day is equivalent in terms of acidity to a liter of hydrochloric acid.

During transport the respiratory gases are mostly in chemical combination with certain constituents of the blood. This makes it possible to move 100 to 150 times as much oxygen and carbon dioxide as could be moved if they were only dissolved in the blood. Each gas must, however, exist in simple solution on its way to the carrier compound and upon its release from that compound. In man about 99 per cent of the oxygen is carried in a loose sort of chemical combination with hemoglobin, an iron-containing protein found in red blood cells. The combination is called oxyhemoglobin and is responsible for the red color of oxygenated blood. During normal ventilation of the lungs, an individual has about 97 per cent of his hemoglobin saturated with oxygen. With forced breathing the percentage of oxyhemoglobin rises. At high altitudes, or in certain diseased conditions, considerably less saturation of hemoglobin is possible, and the amount of oxygen supplied to the cells is inadequate. Corrective measures must be taken in order to obtain sufficient oxygen. Animals living at high altitudes make more red blood cells, thereby supplying more oxygen carriers. In an airplane or in case of disease, the concentration of oxygen in the air breathed can be raised. The increased concentration results in higher pressure which drives more oxygen through the respiratory membrane into the blood. At the capillary level in the tissues, hemoglobin gives up its oxygen and is known as reduced hemoglobin; this gives the blood a purplish color.

Gas exchange now occurs between the blood and the cells through the endothelium of the capillaries. The freed oxygen in simple solution diffuses through the lymph into the cells to take part in biological oxidation. The movement of oxygen into the cell and carbon dioxide from it obeys the rules governing gas exchange in the lungs. The pressure gradient for oxygen in the tissues is from blood to cells; the gradient for carbon dioxide is from cells to blood.

About 92 per cent of the carbon dioxide is carried in the blood in chemical combination, most of it as bicarbonate. The red blood cells contain an enzyme which accelerates the combination of carbon dioxide and water to form carbonic acid. Carbonic acid then dissociates, and about a third of the bicarbonate ions form a salt with potassium in the red blood cell. The other bicarbonate ions diffuse out of the red blood cell and form either a sodium salt or more carbonic acid. In this way, the excreted carbon dioxide is processed by the red blood cells and then transported to the lungs. There it goes into solution and is eliminated by diffusion.

Excretion

Continuity of chemical reactions depends on the removal of their end products. Consequently, the waste products of metabolic reactions, or **excreta** of the body, must be continuously removed from cells in order that metabolic reactions may continue; the waste products diffuse from the cells into the blood stream. The process of removal of waste products of metabolism from the body is called **excretion**; the important organs of removal are the lungs, skin, excretory organs, and liver. It will be recalled that the waste products of cellular metabolism are carbon dioxide, water, and nitrogenous compounds.

The excretion of carbon dioxide in the lungs of terrestrial vertebrates has already been discussed. In aquatic animals this waste gas diffuses into the water surrounding the gills. Also, the relatively thin, moist skin of the amphibia excretes considerable amounts of carbon dioxide.

Water is excreted by a number of organs. Exhaled air is moist because the lungs of air-breathing vertebrates excrete water. In the skin of many mammals, including man, there are sweat glands from which watery solutions pass to the outer surface of the body by way of ducts (Fig. 3.25). Sweating, however, is of less importance as an excretory process than it is in the regulation of body temperature (p. 125). In the majority of vertebrates at least 50 per cent of the water is excreted in the urine through the ducts of the kidneys.

The kidneys in man account for only 0.4 per cent of the total body weight. Yet they handle in 1 day about 180 liters of fluid containing in solution solids

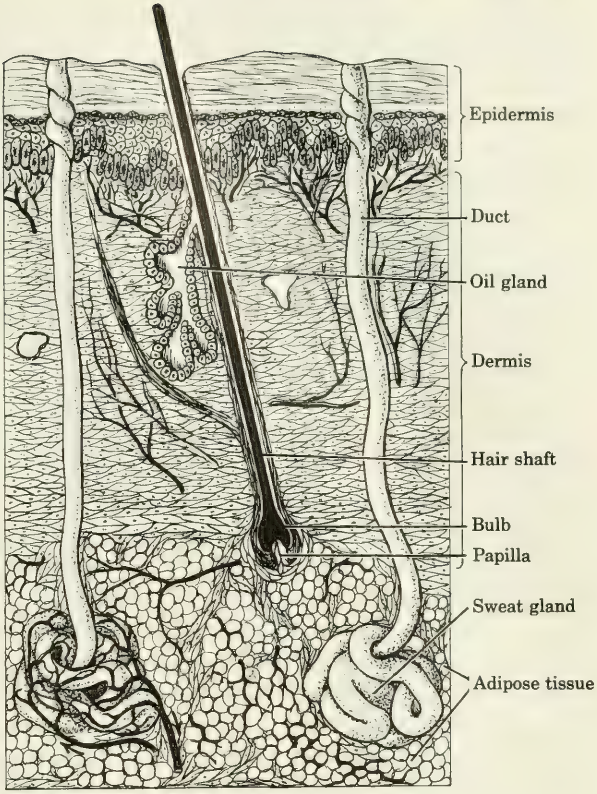


Fig. 3.25. The skin of man, in section, showing characteristic structures; diagrammatic. The bulb is the so-called root of the hair, where growth occurs. Blood vessels and nerves associated with the hair are found in the papilla. Capillaries are shown around the sweat gland at the left but are dissected away on the right.

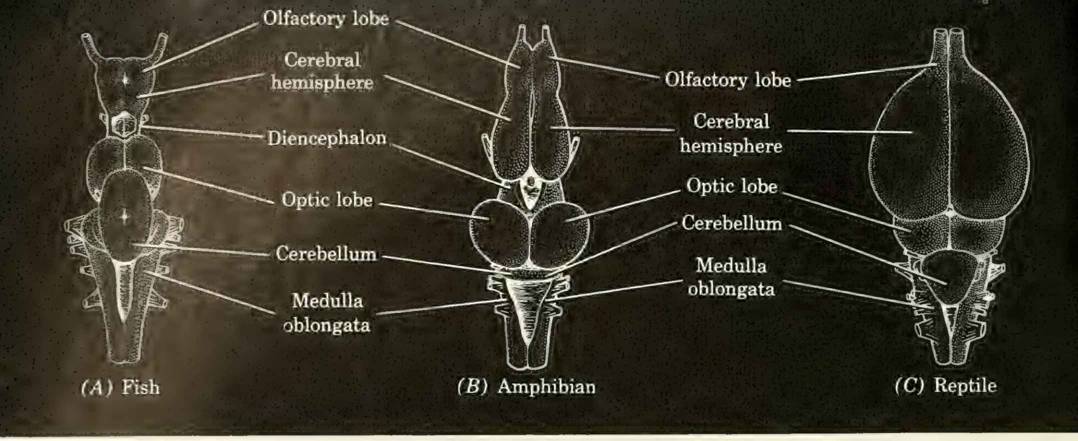
weighing nearly five times as much as the kidneys. Each kidney in man is made up of approximately a million structural and functional units, the **nephrons** or excretory tubules (Fig. 3.12). The arrangement of the blood vessels of the nephron is unique and makes possible its function of excretion. A short arteriole carrying blood from the renal artery is continuous with the glomerulus, which is a tuft of capillaries with few anastomoses. Blood is forced through the glomerular capillaries into another arteriole of about the same diameter as the entering one. Under such circumstances, pressure **filtration** of the blood occurs for as long as it remains in the glomerulus; about one-fifth of the plasma entering the glomerulus is filtered out into the lumen of the nephron. All the constituents of the blood plasma except the large protein molecules can pass through the capillary wall and the epithelium of Bowman's capsule.

Blood from the outgoing arteriole of the glomerulus passes into a capillary bed which surrounds the excretory tubule, which is very long and convoluted in the kidneys of mammals. The difference in concentration between the glomerular filtrate and the blood in the capillary bed results in the **reabsorption** by the blood of most of the material removed in the glomerulus. About 99 per cent of the water is reabsorbed, thus concentrating the filtrate which is now known as **urine**. The amino acids and inorganic ions (Na^+, K^+, Cl^-, HCO_3^-, $HPO_3^=$, and $SO_4^=$) also re-enter the blood by diffusion, as does about 40 per cent of the urea. Urea, $CO(NH_2)_2$, is the chief nitrogenous waste of mammals and results from amino acid metabolism. It is built up in the liver in a series of reactions, driven by the energy of ATP, and directed by at least seven different enzymes. Glucose moves back as a result of active transport (p. 74); that is, energy is required to move it across the membrane of the tubule. Only transitorily after a meal rich in carbohydrates, or in the diseased state of diabetes (p. 120), can glucose be found in the voided urine. Cells of the tubular membrane also add certain substances to the tubular fluid. In addition to the waste products of metabolism, certain drugs, such as penicillin, and compounds detoxified by the liver leave the body in the urine. The kidneys function in the manner indicated to preserve the constancy of the internal environment of the animal with respect to water and electrolyte balance which is necessary for optimal body function, as well as to eliminate nitrogenous waste products of metabolism.

There are substances other than those we have just discussed which must also be eliminated if the organism is to remain normal. One of these is the pigment bilirubin, formed by the disintegration of hemoglobin when red blood cells die and are destroyed. Bilirubin leaves the body by way of the liver and is the pigment chiefly responsible for the color of the bile. Jaundice results if for any reason this pigment remains in the body. The liver also eliminates cholesterol, which arises, in part, from the destruction of red blood cells. Certain types of gallstones are almost pure cholesterol, which is a steroid (p. 26). Various drugs, certain poisons, and metals, such as copper and iron, none of which are excreta as we have defined the term, are eliminated from the body in the bile secreted by the liver. These substances are dissolved in the bile and are carried to the large intestine, where they are found in the feces and eliminated when defecation occurs.

Summary

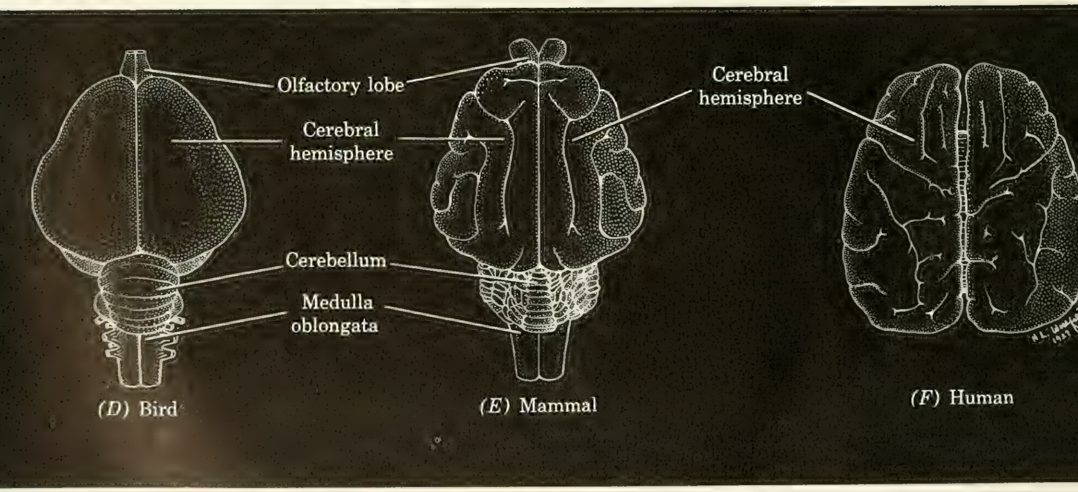
In this chapter, we have considered the ways in which multicellular animals like the vertebrates have met the metabolic requirements of the living cells of which they are composed. We have described systems of organs—digestive, circulatory, respiratory, and excretory—the functions of which, in the final analysis, are simply to provide an internal environment in which individual cells, specialized in many different ways, can maintain themselves and contribute to the life of the whole group. It may have occurred to you that in such a complex and interrelated series of events there must needs be some insurance of orderliness, of checks and balances, because externally the individual animal appears to us as a unit. The unification or coordination of the many functions you have learned about in this chapter is the contribution of other cells and organs, the nature of which will be discussed in the next chapter.


Olfactory lobe
Cerebral hemisphere
Diencephalon
Optic lobe
Cerebellum
Medulla oblongata
(A) Fish
(B) Amphibian
Olfactory lobe
Cerebral hemisphere
Optic lobe
Cerebellum
Medulla oblongata
(C) Reptile

CHAPTER 4

RESPONSIVENESS IN VERTEBRATES

Fig. 4.1. Brains of representative vertebrates, from dorsal view.


Olfactory lobe
Cerebral hemisphere
Cerebellum
Medulla oblongata
Cerebral hemisphere
(D) Bird
(E) Mammal
(F) Human

The organ systems related to metabolism perform certain functions which are necessary if individual cells are to remain alive. They deliver food and oxygen to all cells and remove their waste products, providing a suitable internal environment for maintenance and function of the different tissues. The stability of the internal environment, upon which our feeling of well-being depends, requires constant adjustment of the interlocking functions. The many systems must work together, or be coordinated. If any system concerned with the metabolic needs of cells ceases to function, the organism cannot remain alive; it becomes abnormal if the activities of its organs are not correlated in the usual way.

Although we are not conscious of the regulation of our internal environment, we are well aware of many of the adjustments we necessarily make to our external environment. Every mechanism of regulation, adaptation, or coordination, whether conscious or unconscious, is possible because protoplasm has the capacity of responsiveness; a cell responds by internal reaction to a stimulus, or change in its environment. There are two ways of altering the immediate environment of cells in the vertebrate body. One is by means of impulses that pass along the nerves which penetrate to every part of the animal, and the other is by means of substances that circulate in the blood. **Nervous coordination** is brought about by the activities of the sense organs and nervous system. The secretions which enter the blood from the endocrine or ductless glands make what is known as **chemical coordination** possible.

We shall first review the structure of the systems related to coordination and then explain the ways in which they function. These systems are the nervous system, together with the organs of special sense, skeletal system, muscular system, and endocrine system. The skeletal and muscular systems are discussed here because so many adaptive responses to the external environment involve bodily movements for which the nervous, muscular, and skeletal systems are responsible.

Organ Systems Related to Coordination

The Nervous System. The nervous system of vertebrates is divided for purposes of discussion into two parts: the central nervous system and the peripheral nervous system. The **central nervous system** is composed of the brain and spinal cord. The **peripheral nervous system** consists of the nerves which connect the brain and spinal cord with all parts of the body.

The Central Nervous System. The central nervous system develops in the same way in all vertebrates. Soon after its first appearance it is found to have five regions in the brain, which can be distinguished from the spinal cord. These five regions are known, from anterior to posterior, as the telencephalon, diencephalon, mesencephalon, metencephalon, and myelencephalon (see Fig. 5.21, p. 156). None of these parts is lost in any vertebrate, but differences in the degree of development of certain regions, especially of the telencephalon

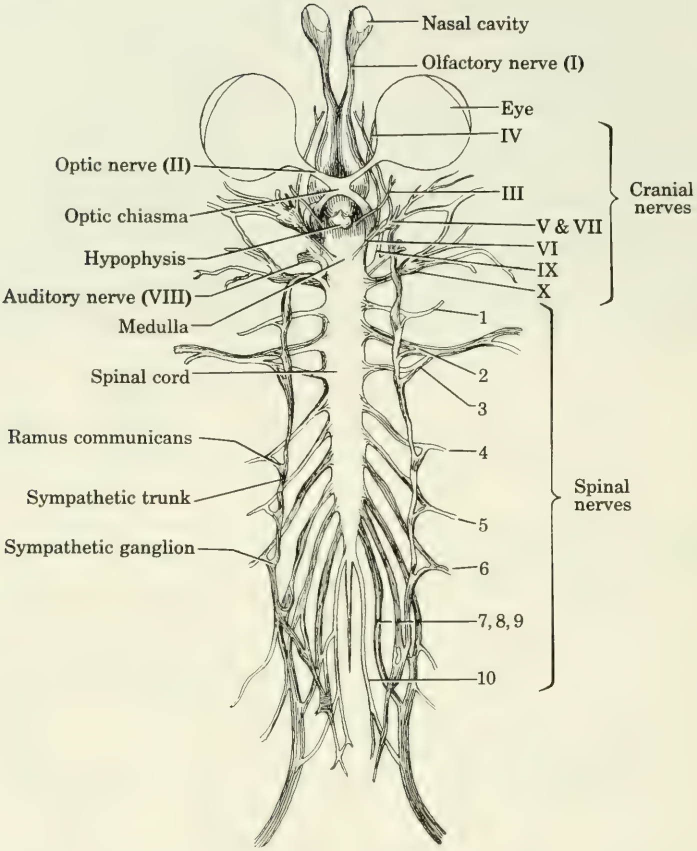

Nasal cavity
Olfactory nerve (I)
Eye
IV
Optic nerve (II)
III
Cranial nerves
Optic chiasma
V & VII
Hypophysis
VI
IX
Auditory nerve (VIII)
X
Medulla
1
Spinal cord
2
3
Ramus communicans
4
Sympathetic trunk
Spinal nerves
5
Sympathetic ganglion
6
7, 8, 9
10

Fig. 4.2. Nervous system of the frog, from ventral view. (Redrawn from R. Wiedersheim, *Comparative Anatomy of Vertebrates*, copyright 1907 by The Macmillan Co., printed by permission.)

and the metencephalon, characterize different classes of vertebrates. The cerebral hemispheres develop from the dorsal part of the telencephalon, and the cerebellum arises from the dorsal part of the metencephalon. Figure 4.1 shows the relative development of cerebral hemispheres and cerebellum in different vertebrates. It will be noticed that the brain of man seems to be composed of only cerebral hemispheres, because they have overgrown the other parts of the brain (see Fig. 3.1, p. 46).

One of the distinguishing characteristics of the phylum Chordata, to which the vertebrates belong, is the presence of a dorsal, tubular, central nervous system. The brain and spinal cord of vertebrates contain a continuous cavity, which is expanded to form the **ventricles** of certain regions of the brain and is reduced to the microscopic **central canal** in the spinal cord. The **anterior** and **posterior choroid plexuses** are composed of the thin roofs of the diencephalon and medulla oblongata, respectively, together with the highly vascularized **pia mater,** the innermost of the membranes surrounding the brain. These rich vascular beds are carried into the cavities of the third and fourth ventricles by the downgrowth of the thin-walled regions. An extension of the anterior plexus passes into the ventricle of each cerebral hemisphere. The cavity of the central nervous system is filled with the **cerebrospinal fluid,** which is chiefly filtered from the blood stream in the plexuses. This fluid also surrounds the brain and spinal cord and has a cushioning, protective function. A slow circulation is maintained, since the cerebrospinal fluid returns to the blood stream by way of the venous channels in the outermost of the brain membranes, the **dura mater.**

The Peripheral Nervous System. The peripheral nervous system is composed of the cranial, spinal, and autonomic nerves (Fig. 4.2). These are bundles of nerve fibers (p. 68) which originate from nerve cell bodies located in the gray matter of the central nervous system or in **ganglia** which are groups of functionally related nerve cell bodies outside the central nervous system. In the brain there are groups of nerve cell bodies similar to the ganglia but called **centers.** In the lower vertebrates, such as the frog, there are ten pairs of **cranial nerves** which are continuous with the brain. All pass to the head and neck with the single exception of the tenth pair, the vagus

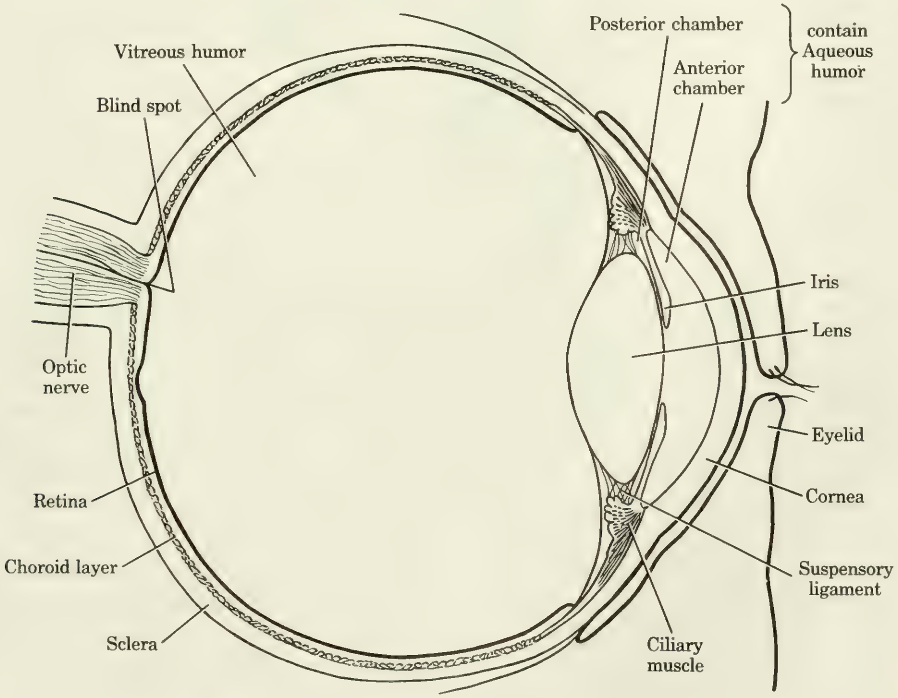

Vitreous humor
Blind spot
Optic nerve
Retina
Choroid layer
Sclera
Posterior chamber
Anterior chamber
contain Aqueous humor
Iris
Lens
Eyelid
Cornea
Suspensory ligament
Ciliary muscle

Fig. 4.3. The human eye in section (cf. Fig. 4.13).

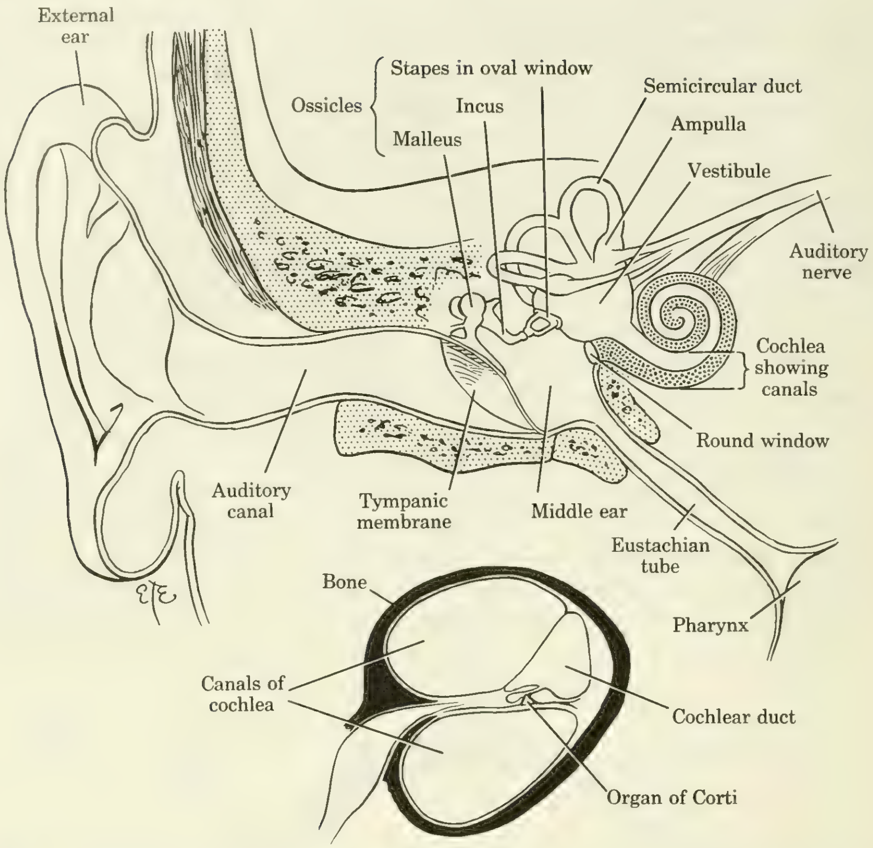

External ear
Ossicles
Stapes in oval window
Incus
Malleus
Semicircular duct
Ampulla
Vestibule
Auditory nerve
Cochlea showing canals
Round window
Auditory canal
Tympanic membrane
Middle ear
Eustachian tube
Pharynx
Bone
Canals of cochlea
Cochlear duct
Organ of Corti

Fig. 4.4. The human ear (cf. Figs. 4.17 and 4.18); the lower figure is a cross section of the cochlea.

nerves, which has branches running to the heart, lungs, and digestive tract. In reptiles, birds, and mammals, eleventh and twelfth pairs of cranial nerves are found. The **spinal nerves** of vertebrates are continuous with the spinal cord and vary in number according to the number of segments in the vertebral column. The spinal nerves extend to the muscles and skin of the trunk and limbs. The **autonomic nerves** are of two kinds, the sympathetic and parasympathetic. The sympathetic nerves originate from that part of the spinal cord located in the thoracic and upper lumbar regions of the vertebral column (see Fig. 4.5). The ganglia which are characteristic of the sympathetic autonomic nerves are located for the most part in paired trunks along each side of the vertebral column. Parasympathetic nerves originate from centers in the midbrain and medulla of the brain and from the spinal cord of the sacral region. Their ganglia are located on or near the organs which they innervate. Autonomic nerves pass to cardiac muscle, to non-striated muscle of blood vessels and coelomic viscera, and to glands.

The Sense Organs. The sense organs or receptors of vertebrates are regions in which certain cells exhibit in a conspicuous manner the capacity of responsiveness in connection with particular changes in the environment. Organs of special sense, such as the eyes, ears, olfactory epithelium, and taste buds, as well as receptors for touch, temperature, and pain are located on or near the surface of the body. In addition to the peripheral sense organs, there are receptors in muscles, joints, and internal organs. It is not our purpose to discuss the structure of any of these organs but to call attention to their relations with the peripheral and central nervous systems. For example, the olfactory nerve extends from the olfactory epithelium of the nasal cavity to the brain, and the optic nerve passes from the retina of the eye to the brain (Figs. 4.2 and 4.3). The auditory nerve connects the sensory epithelium of the inner ear with the brain (Figs. 4.4, 4.16, and 4.17).

The Skeletal and Muscular Systems. The body of vertebrate animals is made up of the **head** and **trunk**; in some, a **neck** and **tail** are present as extensions of the trunk region. Also, in the region of the trunk there are two pairs of **appendages**, fins in aquatic forms and limbs in the terrestrial ones. The skeleton which supports the body of a vertebrate is internal and called an **endoskeleton**. This skeleton serves as a protective case for the central nervous system and as a rigid framework for attachment of the muscles.

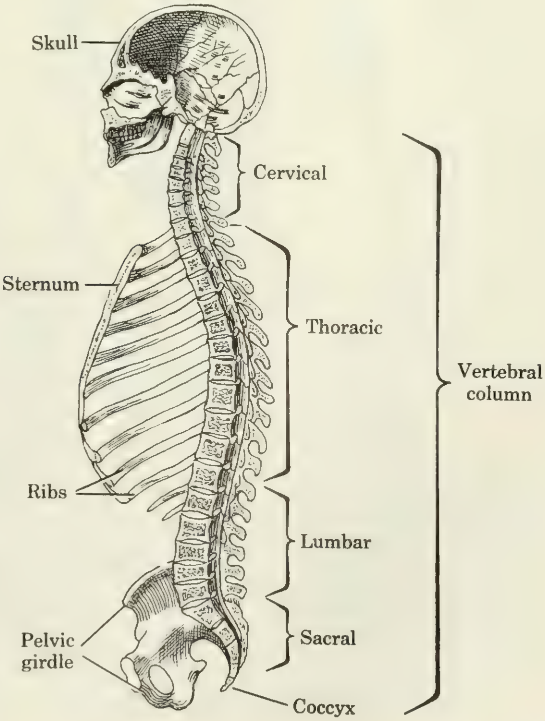


Fig. 4.5. Axial skeleton of man, in lateral view, with skull and vertebral column cut in median section. (Redrawn from T. Hough and W. T. Sedgwick, *Human Mechanism*, copyright 1918 by Ginn and Co., printed by permission.)

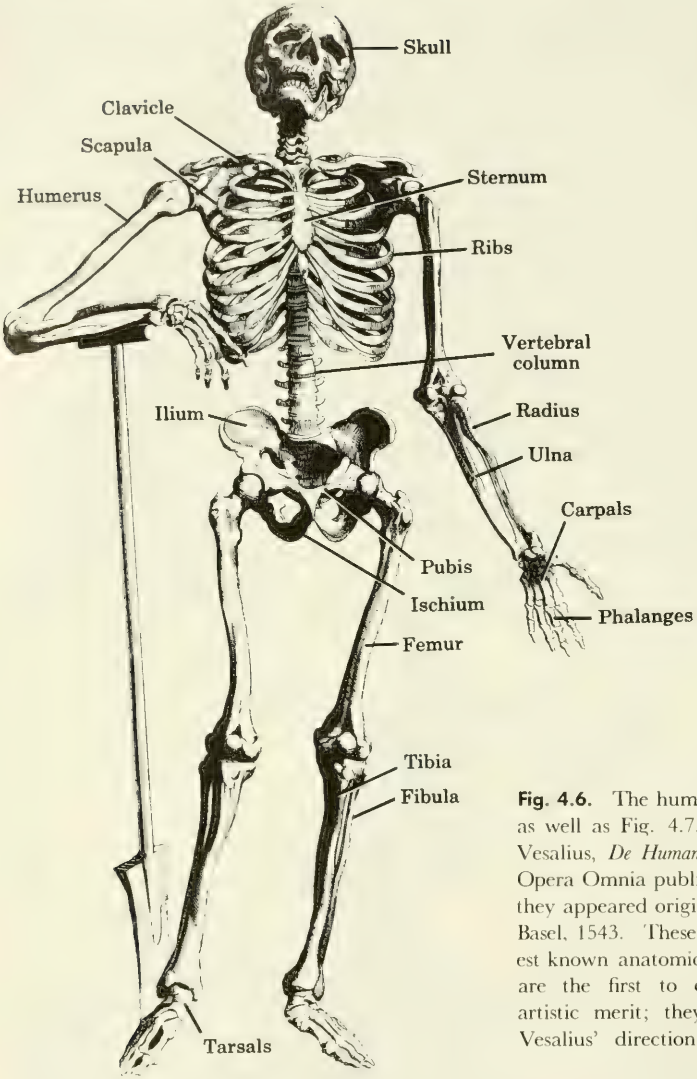

Skull
Clavicle
Scapula
Humerus
Sternum
Ribs
Vertebral column
Ilium
Radius
Ulna
Carpals
Pubis
Ischium
Phalanges
Femur
Tibia
Fibula
Tarsals

Fig. 4.6. The human skeleton. This figure, as well as Fig. 4.7, is taken from Andreas Vesalius, *De Humani Corporis Fabrica* in the Opera Omnia published in Leyden in 1725; they appeared originally in the first edition, Basel, 1543. These figures are not the earliest known anatomical illustrations, but they are the first to combine accuracy with artistic merit; they were prepared, under Vesalius' direction, by pupils of Titian.

The vertebrate skeleton is composed of two main parts, the axial and the appendicular skeleton (Figs. 4.5 and 4.6). The **axial skeleton** includes the **skull**, the skeleton of the head enclosing the brain, and the **spinal** or **vertebral column**, which surrounds the spinal cord. **Ribs** articulate dorsally with the vertebral column and, in birds and mammals, connect ventrally with the **sternum**, or breastbone, in the part of the trunk known as the **thorax**, or chest. The remainder of the trunk region, unsupported ventrally, is the **abdomen**. The skeletal structures of the thorax are sometimes known as the thoracic cage and protect the heart and lungs. Although the skeletons of different vertebrates vary in the number of bones making up the skull and in the number of **vertebrae,** as the bones of the spinal column are called, there is a striking uniformity in the fundamental plan. This uniformity is even more clearly shown in the basic plan of the **appendicular skeleton,** which is made up of the **shoulder** or **pectoral girdle,** the **hip** or **pelvic girdle,** and the bones of the **appendages.** The methods of locomotion in vertebrates are greatly diversified in correlation with the structure of the appendages.

Locomotion is brought about as a result of the activities of the skeletal muscles, which are ordinarily referred to as the **muscular system** (Fig. 4.7).

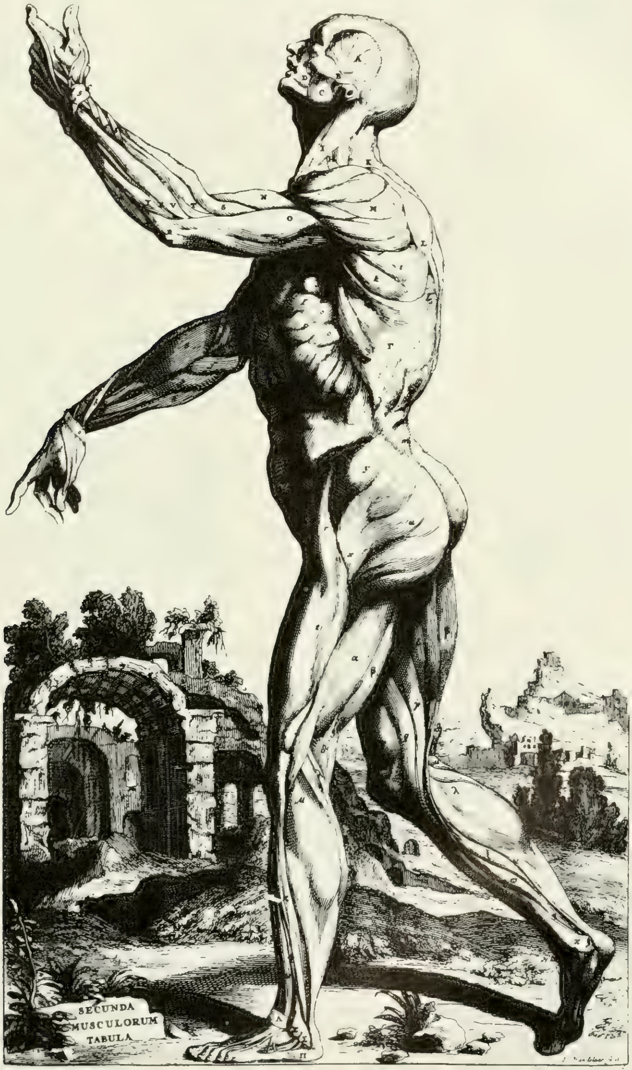


Fig. 4.7. The muscles of man (cf. Fig. 4.6).

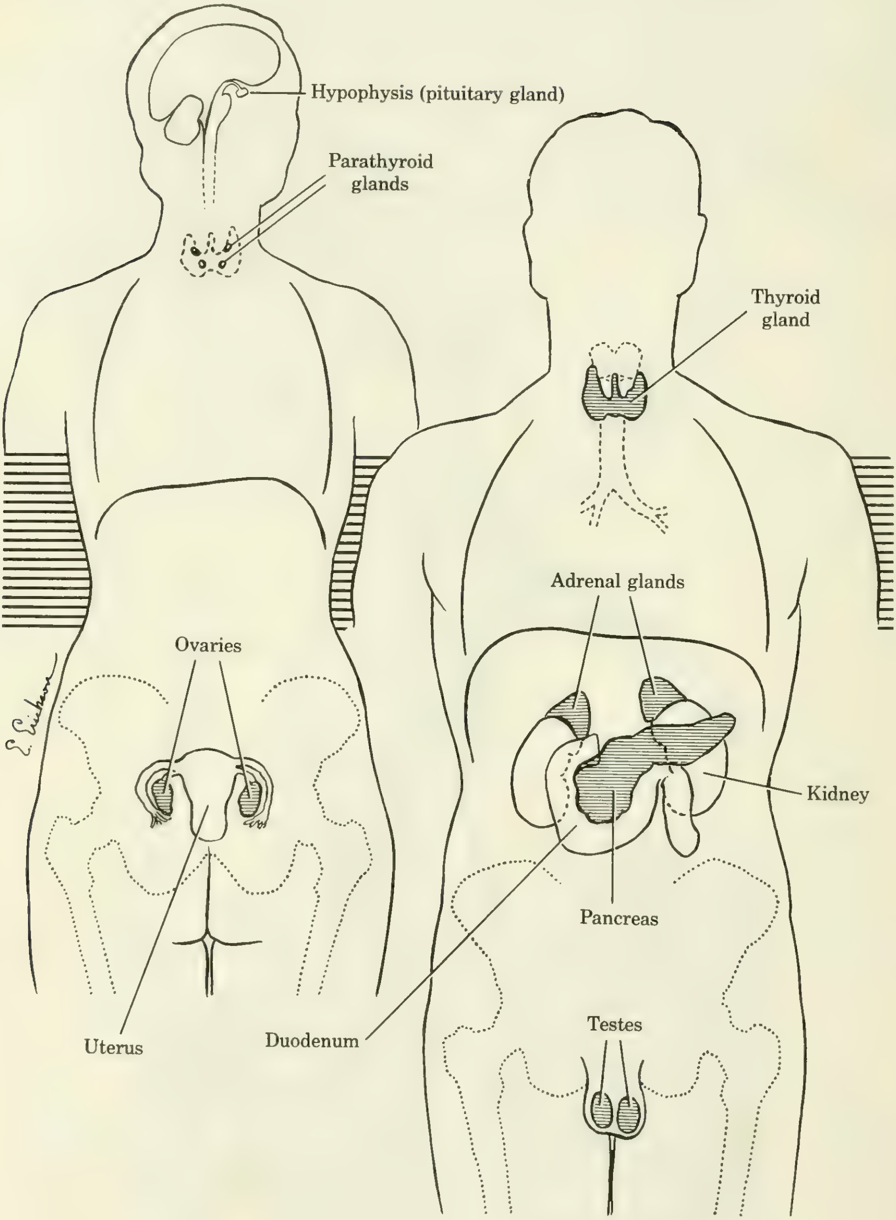

Hypophysis (pituitary gland)
Parathyroid glands
Thyroid gland
Adrenal glands
Ovaries
Kidney
Pancreas
Testes
Uterus
Duodenum
E. Eichner

Fig. 4.8. The endocrine glands of man; with the exception of organs of the reproductive system, the location of these glands is the same in both sexes.

Muscles are attached to rigid bones which are held together at the joints and are characterized by their ability to contract or shorten. By pulling against one another across joints, muscles make possible typical postures, as in man, and when they contract produce locomotion or move the appendages independently. **Joints** of the skeleton of the appendages are freely movable and are of two main types. Hinge joints, which are found between the bones of the upper and lower arm and upper and lower leg, allow movement in only one plane. Ball-and-socket joints, which are found where the bone of the upper arm articulates with the shoulder and the bone of the upper leg articulates with the hip girdle, permit a rotation of the limbs when certain muscles contract or pull against others. The coordination of the activities of the muscles is extremely important for the animal as a whole and is brought about by the nervous system.

The Endocrine System. Reference has been made to glands, or organs of secretion, which possess ducts and pass their secretions onto body surfaces (p. 61). There are a number of glands which do not have ducts by which to discharge their secretions; instead, the secretions pass directly into the blood stream. Such glands are known as the **ductless glands, glands of internal secretion**, or **endocrine glands**. Their secretions are called **internal secretions, endocrines**, or **hormones**. The endocrine system does not consist of a group of closely associated organs like the other systems. Instead, the endocrine glands are widely separated from one another and possess only one feature in common; they pass their secretions into the blood stream. The principal organs of the endocrine system are the hypophysis (pituitary gland), thyroid gland, parathyroid glands (four in man), pancreas, adrenal glands, the gonads, and, in the higher mammals, the placenta (Fig. 4.8). There are, however, several more or less isolated groups of cells, especially in the wall of the small intestine, which also produce hormones.

Coordination with Special Reference to the External Environment

Basic Mechanisms of Nervous Coordination. Every nervous coordination is the result of a reaction by some part of the body to a stimulus. The simplest type of response to a stimulus is known as **reflex action**. When you touch anything hot with your finger, the muscles of your arm react to withdraw your hand. A nerve impulse passes from the point stimulated to the central nervous system and travels back to produce the contraction of the arm muscles. Another well-known illustration is the knee-jerk reflex, in which the leg is extended as a result of a sharp tap below the kneecap. In both these examples the response to the stimulus is apparent in the general region that receives the stimulus. Complete analysis of these simple reflexes shows that they are the expression of a nervous mechanism which some investigators believe explains all nervous coordination.

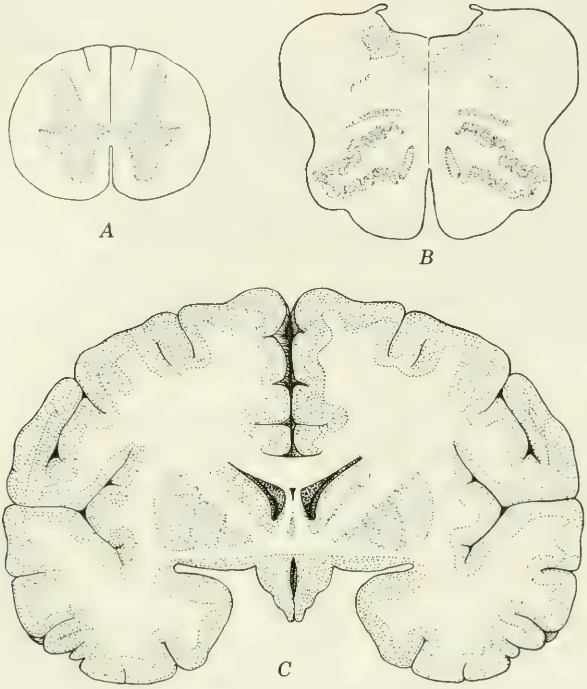


Fig. 4.9. Different regions of the central nervous system, in cross section, to show the distribution of white (clear) and gray (dotted) matter; diagrammatic. *A*, spinal cord; *B*, medulla; *C*, cerebral hemispheres.

The cells of the nervous system that are directly concerned with its function of coordination are known as **neurons** (p. 68). The neurons are arranged in such a way that the parts containing the nuclei are located in groups which constitute the **gray matter** (Fig. 4.9) of the central nervous system and the **ganglia** of the peripheral nervous system. The processes which are always continuous with the main part of the cytosome around the nucleus are called **nerve fibers,** and bundles of them make up the **white matter** of the central nervous system and the **nerves** of the peripheral system.

Many neurons are arranged in what are known as **reflex arcs;** the reflex arc is the cellular mechanism of reflex action. In a reflex arc the ends of the terminal filaments of the axonic process of one neuron (see Fig. 4.22) come in contact with a dendritic process or the cell body of another neuron, but there is no structural continuity between the cells. Such places of contact between different neurons are known as **synapses** and make possible the functional continuity of the nervous system. In the simplest reflex arc there may be only two neurons involved (Fig. 4.10*A*). The stimulus is received by some specialized group of cells constituting a **receptor,** which is a general term for any type of sense organ. As a result of the reception of the stimulus, what is known as a **nerve impulse** is established; this is conducted from the place of stimulation toward the central nervous system along a nerve-cell process (p. 68). In the simplest reflex arc the impulse will be conducted to the

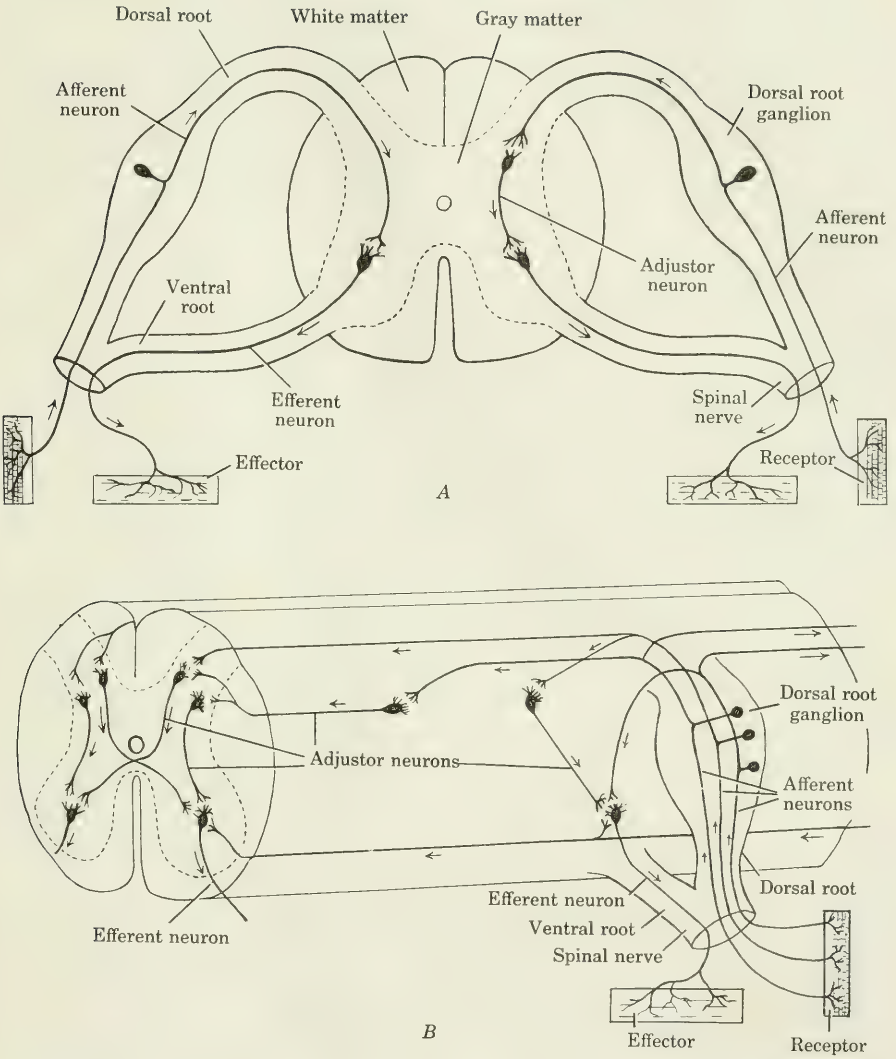

Dorsal root
White matter
Gray matter
Afferent neuron
Dorsal root ganglion
Afferent neuron
Adjustor neuron
Ventral root
Efferent neuron
Spinal nerve
Effector
Receptor
A
Adjustor neurons
Dorsal root ganglion
Afferent neurons
Dorsal root
Efferent neuron
Ventral root
Spinal nerve
Efferent neuron
Effector
Receptor
B

Fig. 4.10. *A*, the spinal cord, in cross section, showing a pair of spinal nerves and the essential parts of a reflex arc; diagrammatic. The neurons necessary for the simplest type of reflex action are shown on the left, and those of a typical reflex arc are represented on the right. *B*, the spinal cord, from the side, showing some relations of neurons in reflex arcs; diagrammatic. The brain would lie to the right as the diagram is constructed. Arrows in both diagrams indicate the direction of conduction of the nerve impulses.

spinal cord. The neuron over which the impulse enters the spinal cord is a **sensory** or **afferent neuron.** The cytosome of such a sensory neuron is located in the **dorsal-root ganglion** of the **dorsal** or **sensory root** of a spinal nerve. One of the processes of the afferent neuron enters the centrally located gray matter of the spinal cord, and its terminal filaments end in contact with other nerve cells found there. In the hypothetical case under consideration, the impulse would pass through a synapse between a process of a sensory neuron and a dendrite or the cell body of a **motor** or **efferent neuron** and leave the spinal cord by way of the axon of the same efferent neuron. This nerve fiber passes into the **ventral** or **motor root** of the spinal nerve and continues to a skeletal muscle, on which it terminates. The place of contact between a nerve-cell process and a muscle cell is known as a **neuromuscular junction** or **motor end plate** (see Fig. 4.22). It is at such a place of contact that the impulse is discharged and a specific chemical compound, acetylcholine, is liberated (p. 115). The muscle is stimulated by the acetylcholine and contracts. This reaction is the effect produced by the change in the environment. A muscle is known, therefore, as the **effector** in a reflex arc. The parts of the simplest type of reflex arc are the receptor, where the stimulus is received; the afferent neuron, over which the impulse is conducted to the spinal cord; the efferent neuron, over which the impulse is conducted away from the spinal cord and from which it is discharged; and the effector, where the reaction to the stimulus occurs.

In the great majority of reflex actions the effect is produced in some part of the body other than that at which the stimulus is received. If the skin of a dog's back is rubbed with a pointed instrument, the animal will respond by attempting to scratch the place of stimulation with its hind leg. The receptors in this instance are located at the roots of the hairs of that region of the back which is stroked. The afferent neurons conduct the impulses to the spinal cord over the dorsal root of the spinal nerve whose fibers extend to that region of the skin. Within the gray matter of the cord each sensory neuron has synapses with neurons of which both the cytosome and processes lie entirely inside the spinal cord. Over the processes of such neurons the nerve impulse is conducted posteriorly along the spinal cord to the level of exit of the nerves that extend to the hind legs. Here synapses occur with efferent neurons, and impulses leave the spinal cord over the ventral root of a spinal nerve and pass to muscles (effectors) that produce the scratching motion.

In this type of reflex arc three kinds of neurons are concerned (Fig. 4.10*A*). The neuron along which the impulse passes within the spinal cord is known as an **adjustor neuron** or **interneuron.** Adjustor neurons are very numerous in the central nervous system and make possible the varied reactions that a single stimulus can produce. For example, when acid is applied to the skin of a frog's back, the first reaction is a contraction of muscles of the body wall in the region stimulated. Very soon, however, this is followed by other reactions which can be observed best in a frog from which the brain has been removed (Fig. 4.10*B*). The fore leg on the side stimulated moves toward the location of the acid, and this reaction is followed quickly by movements of the hind legs on the same side. These movements tending to remove the acid are made possible by the passage of impulses over adjustor neurons which conduct them anteriorly and posteriorly to efferent neurons leading to muscles of the fore and hind legs. The reactions described occur on the side of the animal to which the acid has been applied. If under such conditions the hind leg on this side be held, the muscles of the hind leg on the opposite side will respond to the original stimulus by contracting. This effect is made possible by the presence of adjustor neurons which conduct impulses from one side of the spinal cord to the other and thus bring about bilateral coordination.

In examples given we have been concerned with isolated reflexes; that is, particular reflex arcs have been discussed as if they were separable from the remainder of the nervous system. Such is obviously not the actual state of affairs. During life great numbers of sensory neurons are conducting impulses to the central nervous system at all times. Within the central nervous system, fibers of a number of different sensory neurons may end on the dendritic processes or cell body of a single sensory or adjustor neuron. Different axonic processes of a single sensory or adjustor neuron may end on different adjustor or motor neurons. It has been reported that the cell body of a single motor neuron in the spinal cord of a mammal may have as many as 1800 end feet of terminal filaments on its surface. Over this apparent maze of pathways pass in orderly fashion the nerve impulses that make possible not only simple reflex actions but higher nervous coordinations as well.

The factors which determine the smooth function of the nervous system are complex and not entirely understood. In an organ of special sense there are cells that are much more sensitive to a certain kind of change in the environment than to any other. The response of sensory cells to stimuli apparently involves a change in the permeability of their membranes, modifying the ionic or chemical environment of nerve endings in their vicinity. In some way this brings about excitation of the nerve endings so that their membranes exhibit increased permeability to sodium and potassium ions; the movement of ions results in the establishment of an electric current. This excitation builds up in the nerve endings until a nerve impulse of the so-called **all-or-none** type is touched off and conducted along the nerve fiber in a manner to be described later (p. 112). The more intense the stimulus, the more frequent the initiation of the impulses; the frequency varies from 50 to 100 impulses per second. So long as the excitation is adequate, impulses of uniform intensity are established and travel toward the central nervous system and into all processes of the neuron at an undiminished rate. In the terminal filaments in the region of the synapses the arrival of an impulse, lasting about 1/1000 of a second, is probably associated with the transitory production of acetylcholine (p. 115) which increases the permeability of the membrane of the dendrite or nerve-cell body of the neuron with which the synapse occurs. Local responses at the many synapses on adjustor and motor neurons vary in intensity and are known as **graded responses** in contrast to the all-or-none responses of axonic processes. As a result of the phenomenon of **facilitation,** graded responses in adjustor and motor neurons may be reinforced by the arrival of successive impulses on the same or different sensory neurons until the threshold for firing an all-or-none impulse is reached. When this happens, the pattern of response to the stimulus begins to take shape as the conduction pathways are selected. It is important to understand that the nerve-cell bodies in the central nervous system are kept in a constant state of excitation, the **central excitatory state,** by the arrival of successive impulses from the many sense organs. If the volleys of impulses are frequent enough, the graded responses will build up in a neuron until they trigger the firing of all-or-none impulses in its axonic process. The central nervous system is functionally characterized by its readiness to respond.

The mechanism of the reflex arc obviously makes possible the highest degree of coordination in what is known as the behavior of the animal. Sherrington has generalized the facts of nervous coordination in his **principle of the final common path.** Each afferent neuron is a special pathway by which impulses from its particular receptor enter the central nervous system. Within the central nervous system the impulse can travel over varied paths formed by synapses between adjustor neurons and, theoretically, can produce a reaction in any of the effectors. The efferent neurons, over which impulses travel from the central nervous system to the effectors, differ from the afferent neurons in that they are not private paths for particular impulses. It is a commonplace that many different kinds of stimuli can produce the same reaction or effect. Consider, for example, the many and varied stimuli to which man responds by walking. The efferent neuron is, therefore, a final common path over which impulses established by stimulation of receptors all over the body can be discharged at a particular effector. By means of the adjustor neurons of the central nervous system, connections are made possible between all the special pathways that lead from receptive areas and these final common pathways to effector regions. The conduction of impulses according to this principle of the final common path establishes a mechanism for the complicated and varied responses that characterize nervous coordination. By means of this mechanism the animal can behave as a unit in its reactions to the changing conditions of its external environment and also maintain its internal environment within a narrow range of physiological variation.

Series of reflexes, or their occurrence in sequence, are well understood in some situations and are a very important factor in reflex coordination. The procedure by which a frog obtains its food involves a sequence or chain of reflexes. The visual stimulus produced by a moving insect is followed by protrusion of the tongue. If the insect is captured, its contact with the roof of the mouth cavity initiates the swallowing reflexes, which occur in sequence.

In the examples considered so far, the response to the stimulus has been studied with respect to the usual external conditions that produce the effect. Pavlov, a Russian physiologist, discovered that it is possible to produce what he termed **conditioned reflexes.** For instance, the flow of saliva is a reflex action stimulated normally by the sight of food. Under experimental conditions a bell is rung whenever food is given to an animal. After a number of such experiments the mere ringing of the bell, without the sight of food, will result in the secretion of saliva. In this way a stimulus that originally had no effect upon the salivary glands has become associated with one to which the glands respond. As a result of this association the previously indifferent stimulus of the ringing bell becomes effective in producing the reaction of the salivary glands; a conditioned reflex has been established. Experiments and analysis of conditioned reflexes make it clear that many human reactions are the result of such correlations. Our responses to warning colors, signals, and nationally used signs and symbols are in the nature of conditioned reflexes. The same explanation holds for many more subtle and less well-understood adjustments.

Localization of Function in the Nervous System. The basic mechanisms of excitation and conduction are shared by all parts of the nervous system. Different regions of the nervous system do, however, have certain distinctive functions.

The general function of the **peripheral nervous system** is to conduct nerve impulses to and from the central nervous system. In regard to the spinal nerves, it has been pointed out that processes of afferent neurons enter the spinal cord over the dorsal roots of spinal nerves, and the processes of efferent neurons pass out along the ventral roots. The spinal nerves are called mixed nerves and may be considered to represent the primitive condition of nerve trunks. Certain of the cranial nerves, as the third or oculomotor, also carry processes of both sensory and motor neurons. Other cranial nerves carry processes of but one type of neuron. The eighth cranial or auditory nerve is made up entirely of processes of afferent neurons from the ear; the eleventh and twelfth cranial nerves, found in the higher vertebrates, contain processes of only efferent neurons. Finally, the autonomic nerves are entirely efferent and constitute the final common paths to glands and to non-striated muscles of the blood vessels and viscera.

As has been repeatedly implied in the discussion of the reflex arc, the general function of the **central nervous system** is the adjustment of incoming to outgoing impulses. It is in the central system that afferent neurons have synapses with adjustor neurons, and these in turn with efferent neurons. The multiplicity of connections thus made possible furnishes the most important part of the mechanism of integration.

Adjustor neurons in the **spinal cord** are related to the simpler and less complicated of the reflex arcs. In the scratch reflex, for instance, adjustor neurons carry the impulse posteriorly in the spinal cord or conduct it from side to side. Impulses entering the cord over spinal nerves can also pass anteriorly to the medulla, cerebellum, and diencephalon. The cytosomes of these adjustor neurons are located in the gray matter of the spinal cord; their processes, over which impulses are conducted along the cord, are to be found in the white matter. The white matter also contains groups of nerve processes which arise from the cell bodies of adjustor neurons located in the cerebral hemispheres, mesencephalon, and medulla. The gray matter of the cord is, therefore, the location of adjustor neurons which connect different levels of the cord with one another and with parts of the brain and which conduct impulses from one side of the cord to the other. In addition, the cell bodies of efferent neurons, the processes of which pass out in the ventral roots of spinal nerves, are found in the gray matter of the cord. Simple reflexes are adjusted in the spinal cord, and impulses are conducted to and from the brain.

The primitive brain, or brain stem, is composed of the telencephalon, diencephalon, mesencephalon, metencephalon, and myelencephalon (see Fig. 5.21, p. 156). Changes in the direction of greater brain complexity occur chiefly in the regions of the telencephalon and metencephalon, from which the cerebral hemispheres and the cerebellum, respectively, develop. The cerebral hemispheres and cerebellum are the parts in which new functions are added; the functions of the brain stem remain practically constant throughout the vertebrate group. In contrast to its arrangement as a column in the spinal cord, the gray matter occurs in the brain in masses known as **centers,** which may be surrounded completely by white matter, as in the medulla, or form a continuous peripheral layer, as in the cerebral cortex (Fig. 4.9). It is impossible to present here a detailed account of the functions of the parts of the brain, but the more important localizations will be given.

The **medulla,** into which the spinal cord merges, serves as a pathway between the cord and other parts of the brain. It also contains the centers that adjust the reflexes of the tongue and of breathing. In the tongue reflexes, impulses enter over processes of afferent neurons by way of the fifth and ninth cranial nerves and pass out over processes of efferent neurons by way of the twelfth nerve. The adjustor neurons lie in centers within the medulla. The respiratory reflex depends on the sensitivity of the respiratory center in the medulla to the amount of carbon dioxide in the blood (p. 124). Impulses are conducted over processes of efferent neurons to muscles between the ribs and in the diaphragm. The rhythm and depth of breathing and other reflexes of the viscera, pharynx, and larynx are also adjusted in the medulla.

The ventral part of the **metencephalon** consists of fiber tracts that conduct from side to side, as well as of those connecting lower and higher levels. In the **cerebellum,** or dorsal part of the metencephalon, there are important muscle-coordinating centers. These coordinations may involve the body as a whole, as when reactions occur in response to stimuli received by the organs of equilibration, the semicircular ducts of the ear. The adjustments that result in bilateral muscular coordinations are also made in the cerebellum. Such bilateral coordinations are chiefly those of the movements of the limbs, although the muscles of the eyes, facial expression, and mastication are believed by some investigators to be bilaterally correlated in cerebellar centers.

On the dorsal surface of the mesencephalon are found the **optic lobes;** here are located centers in which certain important visual reflexes, such as the constriction of the pupil of the eye in response to the stimulus of light on the

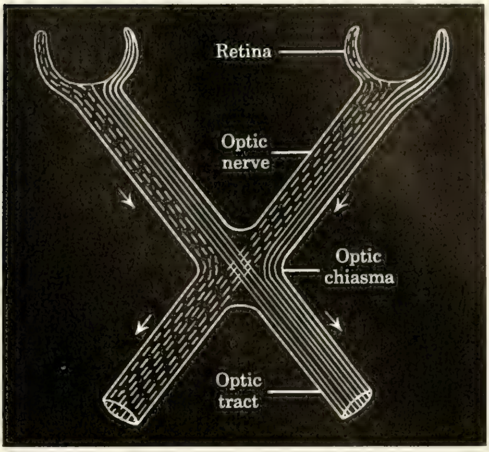


Fig. 4.11. The optic chiasma in higher vertebrates; diagrammatic.

retina, are adjusted. In the higher vertebrates certain reflexes following sound stimuli are also adjusted in the optic lobes. The lateral and ventral regions of the mesencephalon contain groups of neurons that provide for numerous connections and nerve tracts over which impulses are relayed from one region to another.

In the **diencephalon** are found many nerve tracts connecting centers in other parts of the brain with the cerebral cortex. The optic nerves and tracts over which impulses are conducted from the retinas to the optic lobes form part of the floor and lateral walls of the diencephalon. In the lower vertebrates all the fibers from one retina cross the optic chiasma to enter the opposite optic lobe. The crossing in higher vertebrates involves only the medial half of the fibers of each retina; the fibers of the lateral halves do not cross (Fig. 4.11). Certain correlations resulting from olfactory stimuli are made in the diencephalon, and impulses giving rise to pain sensations are received there. Centers concerned with the regulation of many basic vital processes such as sleep, water balance, and heat control are located in the hypothalamus or floor of the diencephalon (p. 125).

Among the lower vertebrates the most important parts of the **telencephalon** are the centers for correlation of impulses transmitted from the olfactory organs. The olfactory centers in mammals occupy the same relative position but are overshadowed by the very great growth of the dorsal part of the telencephalon to form the **cerebral hemispheres.** In the cerebral hemispheres, as in the cerebellum, the neurons that make up the gray matter are found in a continuous superficial layer known here as the cerebral cortex; there are more than 9 billion neurons in the human cortex. Although the cortex is continuous, certain areas are known to be concerned with special functions. Impulses producing movements of the voluntary muscles are conducted from the motor centers of the cortex to opposite sides of the body; that is, if these particular areas are destroyed in one cerebral hemisphere, the animal

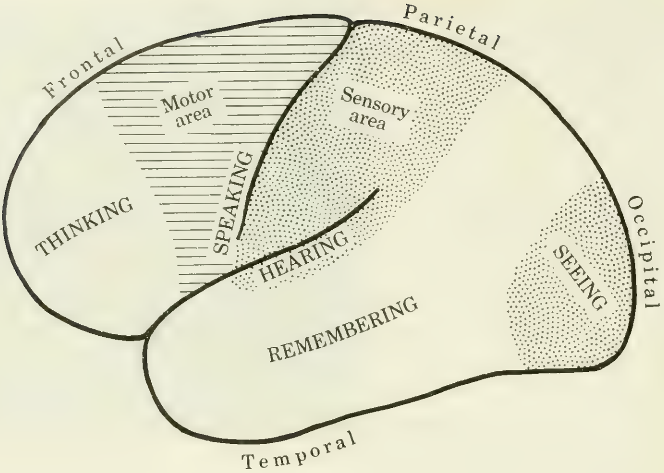


Fig. 4.12. The left cerebral hemisphere of the human brain on which sensory, motor, and association areas are indicated. In the sensory areas (dotted), one or many stimuli are interpreted, as when we identify a typewriter by its sound alone, a lead pencil by handling it, or the type and nationality of an airplane by a synthesis of fleeting visual stimuli. In the motor areas (lined), muscular activities are arranged into purposive or meaningful sequences, as in speaking. The association areas (clear) are concerned with the complex correlations of memory and thought.

is unable to use the voluntary muscles on the opposite side of the body. The regions that coordinate movements of the principal parts of the body, from the toes to the face muscles, are known in man. Another major division of the cortex is concerned with sensory functions and contains the sensory centers to which impulses are conducted from visual, auditory, and olfactory receptors, as well as from receptors of pressure, temperature, and taste stimuli. These areas have been mapped almost completely for the human cortex (Fig. 4.12). The association centers of the cortex are filled with adjustor neurons which are involved in the complicated pathways used in the mental activities of thinking and learning.

Intelligence depends on the degree of development of the cerebral cortex and especially on the neurons of the association areas. An animal's ability to profit by experience involves analysis of a situation and memory, enabling the individual to react in a way that is advantageous in a new situation. This ability is determined by the animal's degree of intelligence, which, in turn, is limited by the number of adjustor neurons and the synapses existing between them. It is known that all the neurons that an animal will ever possess are present at a very early stage of its development. New synapses are, however, formed throughout the life of the individual and probably depend on the variety and intensity of the stimuli received by that individual. The sensory impulses that reach the cerebral cortex, the motor impulses that pass out from it, and the associations made in it constitute our so-called consciousness. Sleep and anesthetics in some way lessen or completely block the functioning of the cerebral cortex and produce unconsciousness.

By combined functions of the nervous system as a whole, the activities of the organism are correlated so that it behaves as a unit; the function of the nervous system is, therefore, coordination or integration. It has been pointed out that nervous coordination depends essentially on three factors. In the first place, the organism must be able to be aware of changes in its environment, that is, to receive different kinds of stimuli. Secondly, nerve impulses which are set up in response to the stimulus are conducted over the neurons of the reflex arcs. And, finally, the animal must respond to the stimulus when the impulse is discharged at some effector. We shall now describe some of the mechanisms concerned with reception, conduction, discharge, and response, especially with respect to adjustment to changes in the external environment.

Reception and Conduction. The **eye** is an organ of special sense containing the **retina** which is made up of cells receptive to changes in the environment brought about by light rays (Fig. 4.3). The cornea, lens, and fluids of the eye function as refracting surfaces which, in the normal eye, bend the light rays entering the eyeball from a distance of more than 20 feet so that they are brought to a focus on the retina (Fig. 4.13). If, during its development, the eyeball grows out of proportion to the refracting surfaces, defective vision will result. The **near-sighted individual** has an eyeball too long for its refracting surfaces, and light rays focus in front of the retina; objects at a distance seem blurred. Contrary to popular opinion, such an individual does not see close objects any better than a normal person does. The **far-sighted person** has an eyeball that is too short for the refracting surfaces, and light rays focus behind the retina; this, too, results in blurred images. If appropriate corrective lenses are placed in front of the eyeball, the light rays can be brought to focus on the retina, and objects are seen distinctly.

When an object is closer than 20 feet, a change in the shape of the crystalline lens of the eye must occur in order for the light rays to be focused on

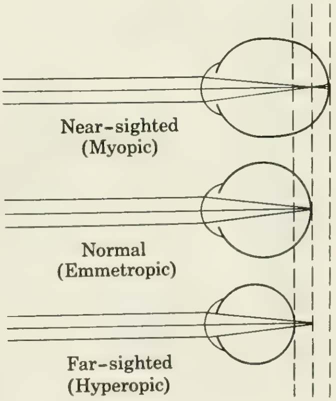


Fig. 4.13. Eyeballs of different shapes; note effect on the focal point for light rays traveling more than 20 feet.

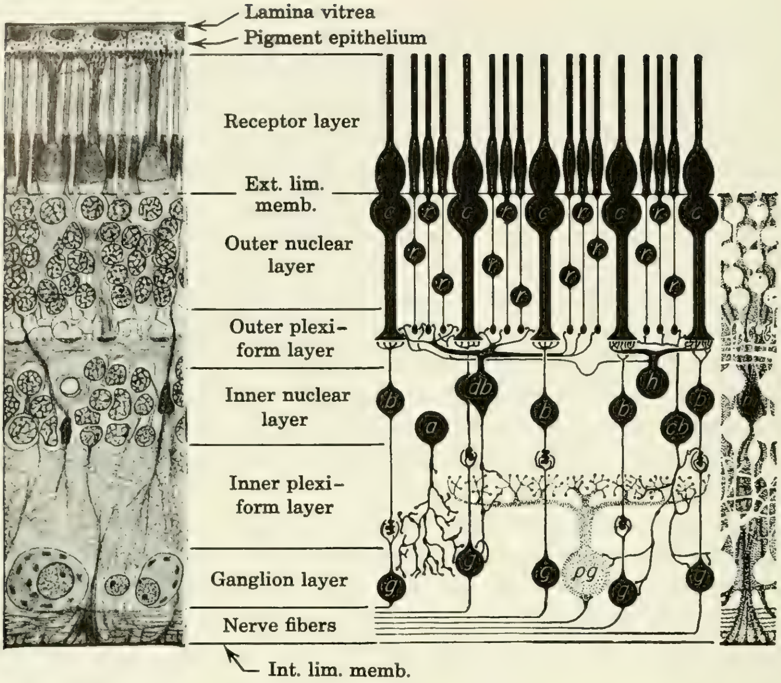

Lamina vitrea
Pigment epithelium
Receptor layer
Ext. lim. memb.
Outer nuclear layer
Outer plexiform layer
Inner nuclear layer
Inner plexiform layer
Ganglion layer
Nerve fibers
Int. lim. memb.
c
r
db
h
b
a
cb
g
pg
M

Fig. 4.14. The human retina (cf. Fig. 4.3). *Left*, drawing of vertical section; the region at the bottom is adjacent to the chamber of the vitreous humor; ×500. *Middle*, diagram showing relationships of principal types of cells. Light passing through the lens, vitreous humor, and inner layers of the transparent retina reaches the receptor layer made up of the outer segments (cf. Fig. 4.15), or photosensitive regions, of the cones (*c*) and rods (*r*). Nerve impulses established in the region called the outer plexiform layer are conducted by way of neurons of different types, the cell bodies of which are shown at *a*, *b*, *cb*, *db*, *g*, *h*, and *pg*. These impulses finally are conducted by way of the nerve fibers which form the innermost layer of the retina and which extend outward through the retina in the region of the blind spot to make up the optic nerve. *Right*, diagram of a Müller fiber (nucleus at *M*), which functions to hold the other retinal elements together; opposite ends of the Müller fibers form the external limiting membrane *(ext. lim. memb.)* and the internal limiting membrane *(int. lim. memb.)*, which lies adjacent to the vitreous humor. (From G. L. Walls, *The Vertebrate Eye*, copyright 1942 by Cranbrook Institute of Science, reprinted by permission.)

the retina. This **accommodation** involves the contraction of the ciliary muscle which releases the tension on the lens capsule and permits the lens to become more nearly spherical. After 40 years of age, there is a gradual loss of the capacity to accommodate in man; this can be corrected by wearing reading glasses.

The retina contains the light-sensitive receptors known as **rods** and **cones** (Figs. 4.14 and 4.15). Rods are exceedingly sensitive to light and are responsible for vision under conditions of dim illumination. The rods of marine fishes and land vertebrates contain a light-sensitive red pigment, rhodopsin, sometimes called visual purple; rhodopsin absorbs light rays and is bleached in the process (Fig. 4.16). In this way, the receptor cell is stimulated, and impulses are conducted to the central nervous system by way of the optic nerve. Complete resynthesis of rhodopsin can occur only in dim light or complete darkness. If there is a deficiency in vitamin A, rhodopsin cannot be reformed and night blindness results. In the rods of fresh-water vertebrates there is a purple light-sensitive pigment called porphyropsin, the synthesis of which depends on a supply of *cis* vitamin A_2, a molecule with a structure slightly different from that of vitamin A; the reaction cycle is like that of rhodopsin. The cones of land vertebrates contain a light-sensitive violet pigment, iodopsin, which has a reaction cycle like that of rhodopsin except that the protein involved is photopsin, not scotopsin. Cones of fresh-water vertebrates contain a light-sensitive blue pigment named cyanopsin and the reaction cycle is like that of porphyropsin except that the protein concerned is photopsin. Cones function under conditions of good illumination and make possible appreciation of fine detail and of color. Certain defects in cones lead to color blindness.

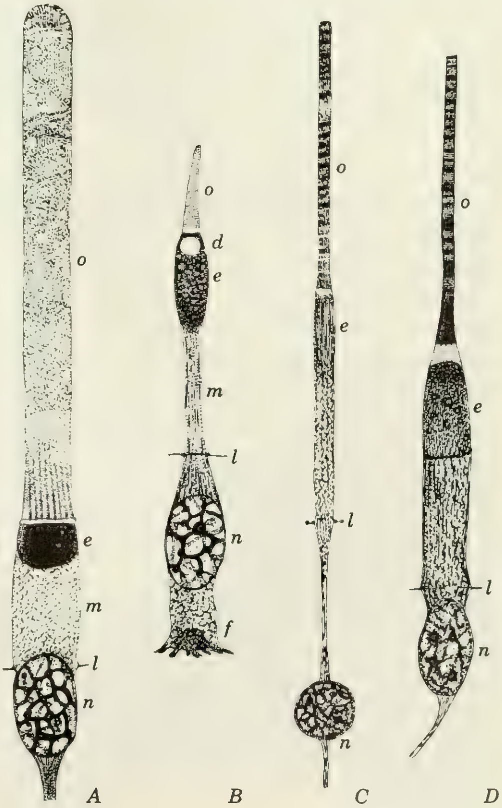


Fig. 4.15. Visual cells of vertebrates; ×1000. *A*, common rod of leopard frog; *B*, common cone of leopard frog; *C*, rod of man; and *D*, cone of man. *d*, oil droplet, typically embedded in *e*, the ellipsoid, which is probably a light-concentrating region; *f*, the footpiece which makes contact with processes of nerve cells in the outer plexiform layer (cf. Fig. 4.14); *l*, position of external limiting membrane; *m*, myoid, a contractile region not present in human visual cells; *n*, nucleus; *o*, outer segment or light-sensitive portion. (From G. L. Walls, *The Vertebrate Eye*, copyright 1942 by Cranbrook Institute of Science, reprinted by permission.)

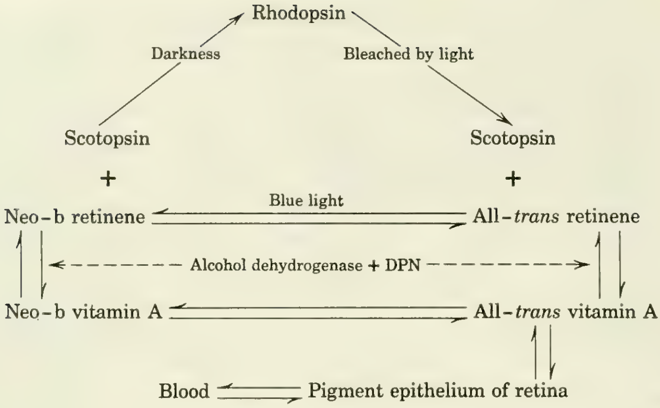


Fig. 4.16. Diagram of the rhodopsin system in the retina of land vertebrates. The visual pigment rhodopsin is formed by the combination of scotopsin, a protein, and retinene, an oxidized form of vitamin A. The molecule known as vitamin A exists in a number of different physical shapes or isomers, each of which can be oxidized to a retinene molecule of the same shape. Only the form known as neo-b retinene can combine with scotopsin to form rhodopsin. When rhodopsin absorbs light, establishing a visual impulse, and the pigment bleaches, the resulting retinene is the all-*trans* form. This may be transformed or isomerized, in the presence of blue light, to neo-b retinene or reduced to all-*trans* vitamin A. Again, this may be isomerized to neo-b vitamin A or lost to the pigment epithelium of the retina (cf. Fig. 4.14) or to the blood. The reversible transformation between vitamin A and retinene is dependent on the enzyme alcohol dehydrogenase and coenzyme DPN, which contains nicotinamide, one of the B vitamins (p. 33). (Adapted from G. Wald, *American Journal of Ophthalmology*, vol. 40, 1955.)

Receptors located in the **inner ear** are of two types: those that respond to changes in position and make possible the maintenance of equilibrium, and those that are sensitive to sound waves and facilitate hearing (Fig. 4.4). During the evolution of vertebrates, these receptors have become localized in different parts of the inner ear. In higher vertebrates, the **semicircular ducts**[1] and **ampullae** of the ear, with their associated receptors, function in maintaining equilibrium (Fig. 4.17). The **cochlea** in these vertebrates contains structures which make possible response to sound waves or vibrations. Sound waves set up vibrations in the tympanic membrane or eardrum. These vibrations are transmitted across the middle ear by way of the auditory ossicles to the so-called round window of the cochlea and produce waves in its basilar membrane (Fig. 4.18). This membrane varies greatly in stiffness along its length, and sounds of different frequencies excite specific regions of it; the highest frequencies set up maximum vibrations in the stiffest portion which is near the window. These localized movements in the basilar membrane bring the surfaces of the hair cells against the tectorial membrane in particular organs of Corti and establish impulses that are conducted to the brain by way of the auditory nerve. How the auditory centers of the brain translate these signals into the call of a bird, a symphony, or the sounds of a city is unknown. Man can detect sounds ranging in frequency from 16 to 20,000 waves per second (middle C is 256 waves per second). Very loud sounds are felt as well as heard and sometimes cause a sense of pain. Exposure to intense sounds may lead to destruction of specific regions of the basilar membrane and so to deafness for tones of the same frequency.

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[1] The term semicircular canals refers to the spaces in the skull occupied by the semicircular ducts.

Vertebrates become aware of chemical substances in their environment if these substances become dissolved in the moist surface of the olfactory epithelium or in the secretions of the mouth cavity. The **nasal epithelium** contains the olfactory receptors which are actually neurosensory cells such as occur in

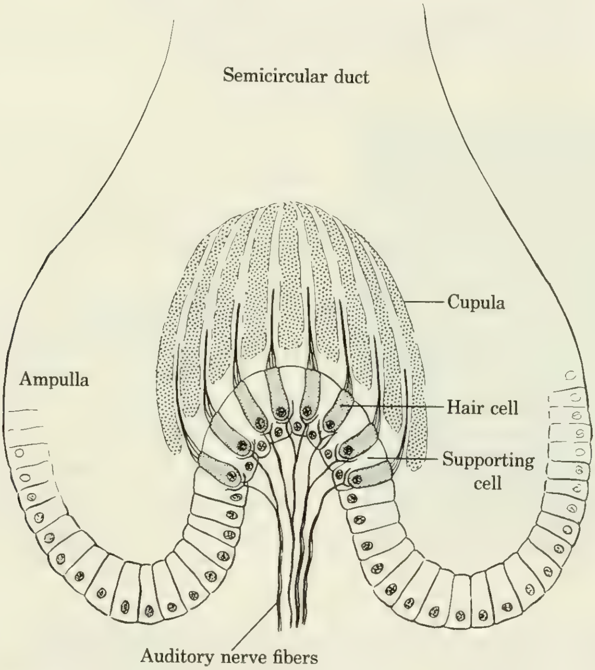

Fig. 4.17. Crista of inner ear; semidiagrammatic. There is a sensory area, or crista, in the ampulla of each semicircular duct (cf. Fig. 4.4). Movement of fluid in a semicircular duct, each of which is located in a different plane, brings about a change of position in the cupula in which extensions from the sensory or hair cells are embedded. Thus the hair cells are stimulated, and an impulse passes over fibers of the auditory nerve toward the brain. Cristae are stimulated by changes in rate of movement of the head and especially by rotational movement. The structure of the **macula**, the sensory area in the utricle of the vestibular portion of the inner ear, is essentially like that of a crista. However, the gelatinous material in which processes of the hair cells are embedded is arranged in a layer known as the **otolith membrane** because it contains small masses of calcium carbonate called otoliths. These respond to gravitational pull no matter what the position of the head; the consequent stimulus of the hair cell makes us aware of the position of the head even when it is not moving. There is a macula in the sacculus of the vestibule, but its function has not been determined.

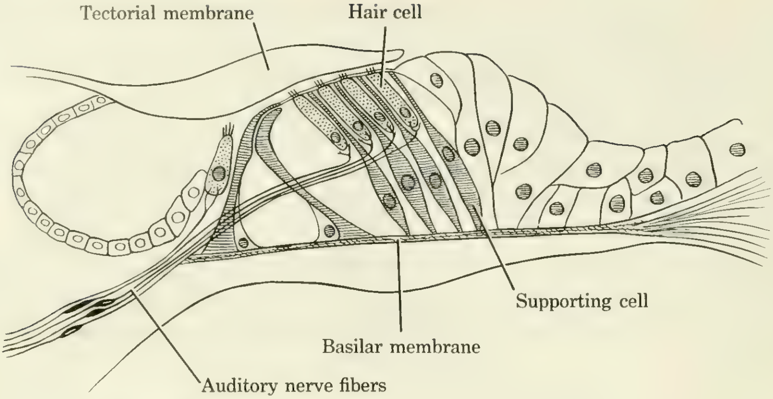
Tectorial membrane
Hair cell
Supporting cell
Basilar membrane
Auditory nerve fibers

Fig. 4.18. Organ of Corti; semidiagrammatic (cf. Fig. 4.4).

many lower animals (Fig. 4.19*A* and p. 523). When the olfactory receptors are stimulated by odors, the impulses that arise are conducted to the brain over processes of the receptor cells. There is a rapid loss of sensitivity on continued exposure to any particular odor, but this does not interfere with responses to other odors.

Taste buds, more widely distributed in aquatic vertebrates, are confined to the tongue in mammals (Figs. 4.20 and 4.19*B*). There are four different kinds of gustatory cells or taste receptors, which makes it possible for man to discriminate four sensations of taste—sweet, sour, bitter, and salty. Taste and smell are inseparable in our reactions to various foods and beverages.

The cutaneous sensations are **touch, temperature,** and **pain.** Receptors for touch are particularly concentrated in the finger tips and are sensitive to slight deformation of the skin in which they are located. There are two types of

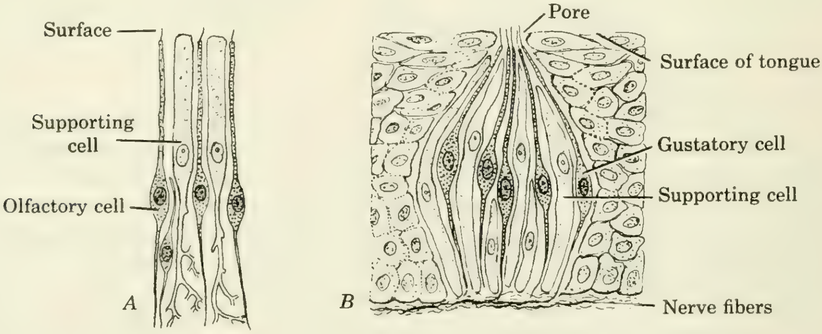
Surface
Supporting cell
Olfactory cell
A
Pore
Surface of tongue
Gustatory cell
Supporting cell
B
Nerve fibers

Fig. 4.19. *A*, cells of olfactory epithelium from the human nose. *B*, cells of a taste bud in epithelium of the tongue. In both cases, the sensory cells terminate externally in hair-like processes that are able to receive the chemical stimuli of olfaction, or smell, and gustation, or taste, respectively.

temperature receptors, one specifically responsive to heat, the other to cold. These receptors are widely distributed but, again, certain areas of the skin contain more of one kind than of the other. For example, the lips are more sensitive to heat than the hands are. Pain receptors are free nerve endings in the skin of the entire body. A wide variety of stimuli result in impulses interpreted by the brain as pain. Local anesthetics, narcotizing the pain receptors, can abolish the sense of pain but leave intact the responses to touch and temperature.

Finally, other receptors are located in deep structures of the body, such as muscles, tendons, joints, and visceral organs. Some of these provide information that is useful in maintaining body posture and in equilibration. Others are important for the maintenance of the normal internal environment of the body by the autonomic nerves; this will be discussed in a later section.

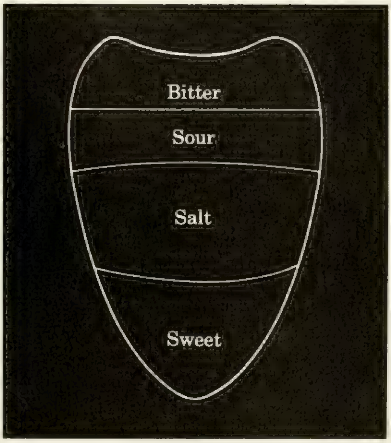

Fig. 4.20. Surface of human tongue, showing areas of localization of taste buds receptive to each of four basic tastes.

Reception, or stimulation of a sensory area, is followed by the establishment of nerve impulses which are then conducted along the processes of the afferent neurons associated with the area. The stimulus must reach a certain intensity before the nerve endings respond. Increased stimulation will increase the frequency with which nerve impulses are initiated in a particular neuron and, also, increase the number of neurons in which impulses start. An increase in intensity of the stimulus above the threshold value does not change the quality of these nerve impulses which are of the all-or-none variety; if the impulse fires at all, it fires at maximum intensity.

The functions of the nervous system require a great deal of chemical energy and exhibit measurable electrical phenomena. When man is in a resting state, about 20 per cent of the oxygen entering the blood stream is utilized in the brain. Less is known about the intricate and very rapid chemical changes than about the closely correlated electrical changes that occur in the

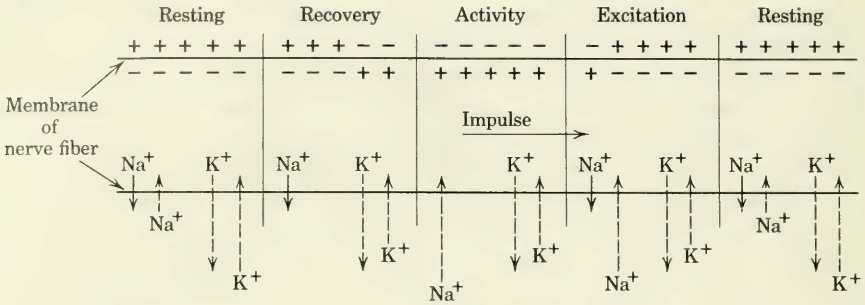

Fig. 4.21. Diagram showing movement of sodium (Na^+) and potassium (K^+) ions across successive regions of the membrane of a nerve fiber as a nerve impulse is conducted. Direction and relative rates of diffusion are indicated by broken arrows, active transport by unbroken arrows.

nervous system. Conduction of an impulse by a nerve fiber is correlated with electrical changes, the magnitude and duration of which can be measured. The electrical properties of a nerve fiber result from its associated ions. When the fiber is not conducting, its interior is electronegative with respect to its surface (Fig. 4.21). Let us assume that a stimulus has been received in a receptor. This activity in the vicinity of a sensory nerve fiber increases the permeability of its membrane. Its electrical properties are changed by a rapid influx of positively charged sodium ions (Na^+), and a nerve impulse starts toward the central nervous system. If the metabolic stores of the nerve fiber are adequate, the current generated by the movement of the ions stimulates the adjacent area of the fiber where similar changes then occur. In this way, the impulse is conducted or propagated along the entire length of the fiber and into all its branches. In the wake of the propagated impulse, positively charged potassium ions (K^+) move out of the fiber, restoring the electrical characteristics of its surface. Also in the restitution phase, the excessive sodium ions are removed from the interior of the fiber by active transport, and it is ready to conduct another impulse, provided its metabolic reserves are still adequate. During the restitution phase the fiber is incapable of responding to a stimulus; it is said to be **refractory.** The refractory period results in a discontinuity in the propagation of impulses along a nerve fiber. In other words, nerve conduction is pulse-like.

An interesting feature of nerve conduction is that the direction in which the impulse moves in the nerve fiber is not reversible under physiological conditions. Afferent neurons always conduct impulses toward the central nervous system; efferent neurons always conduct impulses away from the central nervous system. However, it can be shown that a nerve fiber is capable of conducting an impulse in both directions from the site of an experimental stimulus. The normal unidirectional movement of nerve impulses is determined not by the nature of the nerve fiber but by the nature of the synapse. Impulses can move across a synapse in only one direction.

Depending on the diameter of a nerve and the amount of insulating material it has, conduction velocities vary from 1 to 120 meters per second. Some of the large motor nerves to skeletal muscle in mammals conduct impulses at a rate of approximately 120 meters per second, which is about one-third as fast as sound travels in air.

Discharge and Response. When the impulse arrives at the end of a nerve fiber, a chemical compound known as a **neurohumor** is released. Such a compound is responsible for conduction of the nerve impulse across the **synapse** or junction between two nerve fibers and, also, across the **neuro-effector junction** between the nerve fiber and the effector cell. Depending on the kind of nerve fiber concerned, the neurohumor released will be acetylcholine, epinephrine (adrenaline), or norepinephrine (noradrenaline). The so-called discharge of the nerve impulse occurs at the neuro-effector junction. Release of the neurohumor changes the environment of the effector cell in the region of the junction. Then the effector cell reacts in its characteristic fashion; the change in the environment finally evokes a response of the organism.

Let us consider the sequence of events when a nerve impulse is discharged from the terminal branches of an efferent nerve fiber at neuromuscular junctions, or motor end plates, of the striated muscle cells which such a fiber serves (Fig. 4.22). In responding to the acetylcholine liberated by the motor nerve endings, the permeability of the membrane of the muscle cell is increased; ions move across the membrane into the muscle cells generating an electric current. This **muscle impulse** is passed along the length of the muscle cell in a manner similar to nerve conduction. Sodium ions move in, potassium ions move out, and the energy requirements are met by the metabolism of the muscle cell. The muscle cell, in addition to its capacity to conduct an impulse, is able to contract or change its shape. Muscular contraction consists of a shortening and thickening of the muscle cell and the development of tension. Under resting conditions, some nerve fibers are continually conducting impulses which have been set up in the deep receptors. In response to these, the skeletal muscles are always in a state of slight tension; they exhibit what is called muscle tone. The number of nerve fibers conducting impulses to a muscle is mediated by centers in the brain and depends on the intensity of the stimulus. Analyze for yourself the circumstances under which you shift your position in a chair or race to answer the telephone. Physiologically, a muscle, which is a bundle of muscle cells, is activated by a volley of nerve impulses arriving in rapid succession and eliciting a fusion of twitches, or responses of the individual muscle cells. This results in the smooth, sustained contractions that are responsible for the daily muscular work of the body.

The mechanism of contraction involves two characteristic proteins of muscle, myosin and actin. Under the influence of the muscle impulse, myosin and actin unite to form actomyosin. Myosin also acts as an enzyme which can release the energy in ATP. This powers the shortening and thickening of the actomyosin fibers and, so, of the muscle cell. To provide additional

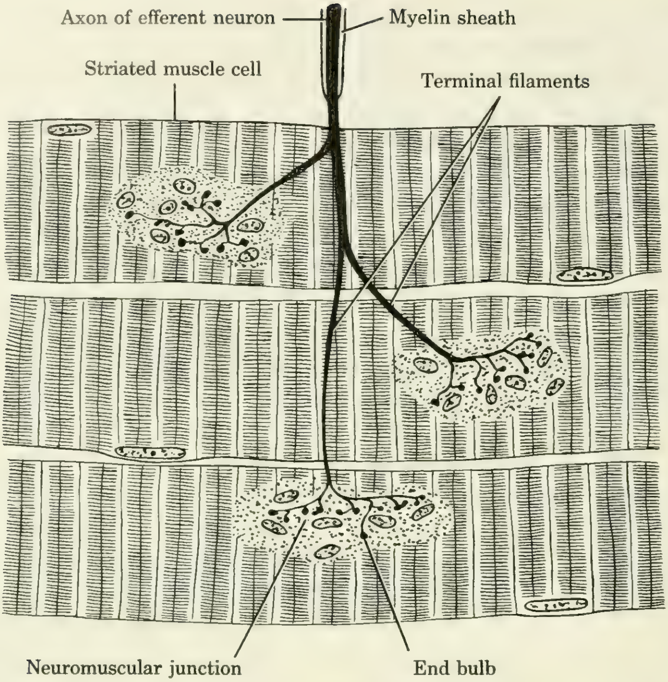

Fig. 4.22. Neuromuscular junctions. The terminal filaments of an efferent neuron may end on specialized areas in a number of different striated muscle cells.

ATP molecules, muscle glycogen is metabolized to lactic acid (p. 36). Some of this is released to the blood stream in man and converted to glycogen in the liver. But most of it accumulates in the muscle cell during muscular work and must eventually be run through the TCA cycle for elimination (p. 36). This is why the oxygen requirement is high during exercise. After contraction, the actomyosin dissociates into actin and myosin and is ready to be reused. An important by-product of muscular contraction in warm-blooded animals is the heat necessary for maintenance of body temperature, under normal conditions as well as under circumstances of excessive loss of heat from the body (p. 125).

Muscular fatigue is a feeling familiar to all of us. We might suppose that it resulted from depletion of the energy stores of the muscle cells or of the nerve fibers innervating them. However, muscle and nerve cells have reserves capable of powering their reactions for relatively long periods of time. The weakest link in the nerve-muscle reaction system is the neuromuscular junction. It does not have the capacity to respond to the discharge of nerve impulses for long periods of time without rest. This is the area that is fatigued by continued muscular work.

Coordination with Special Reference to the Internal Environment

Cellular metabolism, on which life depends, requires a high degree of coordination in the supply of materials and removal of products, whether waste or synthetic. We have discussed in the preceding chapter the major functions of the vertebrate animal that subserve the metabolic requirements of its cells. These varied activities are coordinated in such a way that the environment of individual cells within the body normally varies within narrow limits, no matter what the changes in the external environment may be. If these limits of physiological variation are exceeded, if the regulatory mechanisms fail or are unable to cope with a major emergency, death results.

Two different kinds of organs cooperate in the regulation of the internal environment. These are the autonomic nerves and the endocrine glands. Both can alter the chemical environment of individual cells—the autonomic nerves, like other nerves, by means of neurohumors and the endocrine glands by means of the substances they pass into the blood stream. Interactions between these involuntary coordinators occur in many vital processes, and they can be modified in some cases by emotional reactions and conscious nervous responses.

Regulation by Autonomic Nerves. Gland cells, cardiac muscle, and non-striated muscle of blood vessels, coelomic viscera, and other organs are the effectors served by the division of the peripheral nervous system known as the autonomic nerves. Autonomic nerves are made up of only efferent fibers, two of which are involved in the conduction of any impulse from the central nervous system to an effector. The cell body of the first neuron in the chain of two is located in the central nervous system, and the fiber leaves the central nervous system over the ventral root of a cranial or spinal nerve. This fiber is called the **preganglionic fiber** because it ends in a ganglion which contains the cell bodies of the **postganglionic fibers.** Postganglionic fibers of sympathetic nerves extend some distance from the ganglia of the sympathetic trunks and those among the viscera to blood vessels, glands, and visceral organs. Since the ganglia of the parasympathetic nerves are located on or near the organs served, their postganglionic fibers are relatively short. Sympathetic and parasympathetic nerves also differ from one another with respect to the kind of neurohumor secreted by the endings of their postganglionic fibers. The postganglionic fibers of sympathetic nerves liberate a mixture of two neurohumors known as epinephrine and norepinephrine which are closely related chemically. In this these nerve fibers are unique, since all other nerve fibers, including the postganglionic fibers of the parasympathetic nerves, release acetylcholine. This compound is broken down very rapidly and, consequently, an effector responds for a very limited period to an impulse discharged from a parasympathetic nerve. On the other hand, when sympathetic nerves are excited, impulses are discharged not only in the organ

EFFECTORS	INNERVATION	
	SYMPATHETIC	PARASYMPATHETIC
Salivary glands	Release mucous secretion	Release watery secretion
Cardiac muscle	Increases rate of contraction	Slows rate of contraction
NON-STRIATED MUSCLE BLOOD VESSELS Heart	Dilate	Constrict
Salivary glands	Constrict	Dilate
Pia mater	Constrict	Dilate
External genitalia	Constrict	Dilate
DIGESTIVE TRACT Sphincters	Contract	Relax
URINARY BLADDER Body	Relaxes	Contracts
Sphincter	Contracts	Relaxes
LUNG Bronchioles	Dilate	Constrict
EYE Iris	Dilates	Constricts
Ciliary muscle	Relaxes	Contracts

Fig. 4.23. Responses of effectors dually innervated by autonomic nerves.

innervated but also in the medulla of the adrenal gland. These medullary cells then release epinephrine and norepinephrine into the blood stream; thus, additional amounts of these substances reach responsive effectors all over the body. For this reason, the response to sympathetic discharge is more widespread than that to parasympathetic discharge.

Certain organs supplied by the autonomic nerves receive both sympathetic and parasympathetic fibers and respond in opposite fashion to the continuous flow of impulses from the two sets of fibers (Fig. 4.23). This dual innervation, and the antagonistic responses invoked, constitute the nervous mechanism for subconscious regulation of the activities of vital organs. The response of the organ is determined by the balance in intensity, so to speak, of the opposing stimuli. In general, the reactions to sympathetic outflow, aided by the adrenal medulla, enable the individual to mobilize latent resources in the event of emergencies. Responses to parasympathetic outflow, on the other hand, tend to conserve or restore resources. For example, in the regulation of the rate of heart beat, sympathetic discharge tends to increase the rate, parasympathetic, to slow it down. During an emergency, when increased flow of blood is advantageous, sympathetic discharge predominates over parasympathetic and the heart beats faster. When the emergency is over, the parasympathetic outflow predominates and the heart beat slows to its normal rate.

Regulation by Endocrines. The endocrines, hormones, or internal secretions are the products of the ductless or endocrine glands (Fig. 4.8). Endocrines can produce coordination of a type comparable to that produced by a simple reflex arc, although more often the regulatory effect is widespread. Chemical coordination by means of circulating hormones was discovered by Bayliss and Starling in 1902 in connection with the flow of pancreatic juice into the small intestine. This occurs only when food enters the duodenum from the stomach. It was supposed for a long time that the release of pancreatic juice was conditioned by nervous coordination. Experiments demonstrated that the nerves leading to the pancreas could be cut without affecting the control of the flow of the pancreatic juice when food entered the small intestine. It was then discovered that if the blood vessels are tied so that blood does not enter the capillaries of the pancreas, the juice is not released. Further study revealed that, when the contents of the stomach enter the small intestine, the hydrochloric acid stimulates certain cells in the lining of the duodenum to discharge into the blood an endocrine substance known as **secretin**. Secretin, reaching the pancreas by way of the blood, stimulates the acinar cells of the pancreas to release pancreatic juice, which then passes to the intestine by way of the pancreatic duct. In a similar way, the release of bile from the gall bladder is conditioned by the secretion of **cholecystokinin** from cells in the intestinal lining when stimulated by the acidity of the food mass entering from the stomach. Cholecystokinin is carried to the gall bladder by the blood.

Hormones, like vitamins, are substances required in very small amounts to perform their regulatory functions. Also, like the vitamins, some are protein in nature and others are lipids. Both hormones and vitamins are involved in basic metabolic controls so that dysfunction may be revealed in clinical syndromes. Neither can be stored to any appreciable extent in the body; they must be continuously supplied. But here the similarities end. Animals can synthesize for themselves the compounds we know as endocrines but are dependent on food sources for their vitamins.

The **hypophysis,** or **pituitary gland,** is composed of three parts, the anterior adenohypophysis, the posterior neurohypophysis, and an intermediate lobe. The **adenohypophysis** is exceedingly important in endocrine regulation because its secretions stimulate the growth, differentiation, and normal function of several other endocrine glands; the thyroid, adrenal cortex, and the male and female reproductive organs respond, respectively, to the **thyrotropic, adrenocorticotropic** (ACTH), and three **gonadotropic** hormones. Overall body growth is controlled by the adenohypophysis, presumably by the so-called **growth hormone.** Oversecretion in youth leads to continued growth of long bones and a condition known as gigantism; undersecretion leads to achondroplastic dwarfism. Acromegaly occurs in adults when resumption of bone growth is stimulated as a consequence of hypophyseal oversecretion. Chemical analysis of extracts of the adenohypophysis has yielded several proteins and polypeptides which appear to be the active principles to which the respective target organs are responsive. The action of the hormones that regulate other endocrine glands will be discussed in connection with the target organs. The secretions of the adenohypophysis are known to be regulatory in protein and carbohydrate metabolism, but the exact mechanisms are not so well elucidated as in the case of the vitamins. Regulation of the release of the adenohypophyseal hormones is incompletely understood.

The **neurohypophysis** secretes two hormones, the **antidiuretic hormone** and the **oxytocic principle,** both of which are polypeptides. The antidiuretic hormone promotes the resorption of water from the kidney tubule (p. 83) and thus regulates water balance. If water intake is restricted, the secretion of the antidiuretic hormone is increased, and the urine maximally concentrated. The regulation of release of the antidiuretic hormone is mediated by centers in the hypothalamus. The oxytocic principle induces contraction of the nonstriated muscle in the uterus during late pregnancy; it is widely used to promote parturition. A function for this substance in the normal physiology of the animal has not been established.

The **intermediate lobe** of the hypophysis produces an internal secretion known as **intermedin.** This brings about expansion of the pigment cells in the skin of fishes and amphibia. No function can be ascribed to it in higher vertebrates. It is, you might say, a vestigial hormone.

The **thyroid gland** is essentially a device for the accumulation of iodine, very small quantities of which are present in food in the form of iodides (Fig. 4.24). **Thyroxine** is the iodine-containing amino acid which is the active principle of the complex protein secreted by the thyroid gland. It was

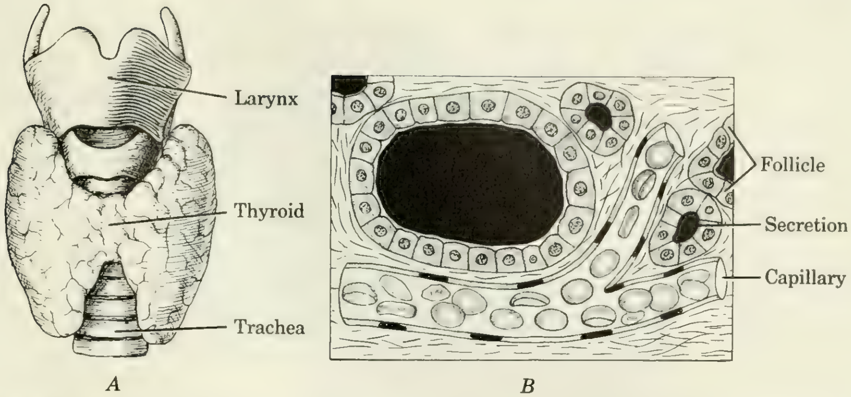

Fig. 4.24. The thyroid gland. *A*, the gland of man as seen from the front, showing its position with reference to the larynx and trachea. *B*, diagram of a section of the gland, showing the follicle cells which produce the secretion and the capillaries which distribute it.

isolated in 1916 and synthesized in 1927. Thyroxine regulates the basal metabolic rate, since it controls the level of cellular oxidation. Current interpretation is that the iodine-containing secretion affects the permeability of the mitochondrial membrane and thus in some way modifies the enzyme team of the mitochondrion (p. 19). Hyperthyroidism, or oversecretion, results in a high rate of cellular oxidation, reflected in rapid heart beat and excitability. Abnormal function of the thyroid gland may bring about its enlargement, forming a goitre. Hypothyroidism, or undersecretion, in children results in stunted physical and mental growth; in extreme cases, the individual is a cretin. In regions where the soil is deficient in iodine, hypothyroidism is endemic. In many parts of the United States the use of iodized table salt is a dietary requirement. The thyrotropic hormone of the adenohypophysis stimulates the production of hormone by the thyroid. If the amount of thyroxin in the blood is adequate, thyrotropic hormone is not released.

The protein secretion of the **parathyroid glands** is related to the control of calcium in the blood. It will be recalled that vitamin D also contributes to this control (p. 31). Calcium is necessary for the differentiation of bone and for the clotting of blood and is required for the normal sensitivity of nerve endings and muscle. Hypofunction of the parathyroids, followed by a lowering of the calcium ion content of the intercellular fluid, results in hypersensitivity leading to convulsive contractions of muscles. When the amount of calcium in the blood plasma falls below a certain level, the parathyroid hormone is released. Its effect is on the kidney tubule where it decreases the amount of phosphate reabsorbed. This results in a reduction of the amount of phosphate in the blood which, in turn, leads to withdrawal of calcium from bone to build up the calcium level of the blood.

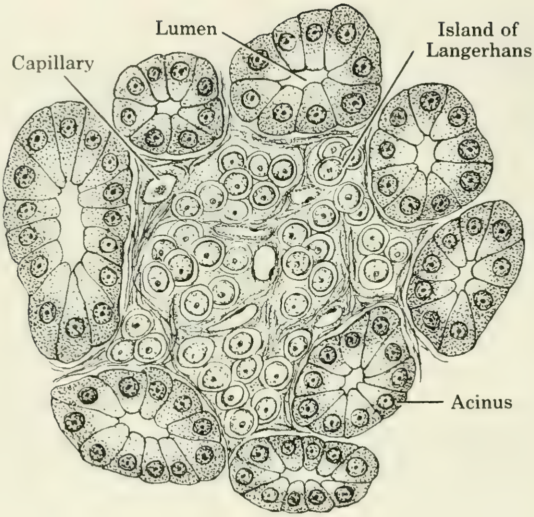

Fig. 4.25. The pancreas, showing an island of Langerhans, the cells of which produce the hormone of the pancreas, surrounded by acini, the cells of which secrete the pancreatic juice; seen in section.

The digestive gland known as the **pancreas** contains groups of cells known as **islands of Langerhans** (Fig. 4.25). These are not involved in the production of pancreatic juice and its digestive enzymes (p. 72); this part of the pancreas is a gland of internal secretion. Histologically, at least two kinds of cells, the alpha or A cells and the more abundant beta or B cells, can be distinguished in the islands. By means of a drug called alloxan, which selectively kills the beta cells, it has been established that they are responsible for the presence in the blood of a polypeptide called **insulin.** This compound was isolated in 1922 and became available in crystalline form in 1927; the 16 amino acids of which it is composed and their arrangement had been determined by 1954. When insulin is absent, glucose is present in the blood in such large amounts that it is eliminated in the urine (p. 84); this is a major symptom of the disease known as diabetes mellitus. Insulin increases the rate at which cells remove glucose from the blood. Continued injections of insulin are effective in controlling diabetes.

The source of another pancreatic hormone named **glucagon** has been localized in the islands of Langerhans. This substance contains 15 amino acids and was not separated from insulin until 1953. It is suspected, but has not been proved, that the alpha cells are involved in its production. Glucagon converts an inactive form of the enzyme phosphorylase to the active form in the liver (see Fig. 2.9, p. 36). This results in the conversion of glycogen to glucose which is released from the liver and raises the blood sugar level. The amount of glucose in the blood is the regulatory factor for release of the pancreatic hormones.

The **adrenal glands** consist of two kinds of cells which in the higher vertebrates are arranged as a central medulla surrounded by a cortex. Both medulla and cortex produce hormones.

The **adrenal medulla** was identified as an endocrine gland in 1901. It is now recognized that the medulla secretes two closely related compounds known as epinephrine (adrenaline) and norepinephrine. These are relatively simple compounds, neither protein nor lipid, and are identical with the neurohumors produced by the endings of the postganglionic fibers of sympathetic nerves. The adrenal medulla, which is innervated by the sympathetic nerves, releases its secretions in response to their discharge and is also very sensitive to emotional stimuli. Epinephrine, like glucagon, activates phosphorylase, but in muscle cells as well as in the liver. In muscle the glucose is available for the energy requirements of contraction. More of the lactic acid produced in muscle metabolism is removed by the blood in the presence of epinephrine. Epinephrine mimics and thus adds to the effectiveness of sympathetic discharge, one effect of which is to increase the rate of heart beat. It will be noted that all these effects tend to make the muscular activity of the individual more efficient. Epinephrine also appears to be effective in bringing about the release of the adrenocorticotropic hormone of the adenohypophysis, another factor in the individual's defense in emergency or stressful circumstances, as will be pointed out later. Norepinephrine acts to constrict capillaries all over the body.

A large number of complex steroid (lipid) compounds have been isolated from extracts of the **adrenal cortex**. A number of the compounds crystallized from the cortex are physiologically active. Their effects fall into two main categories: (1) regulation of salt and water balance (salt-active compounds) and (2) regulation of carbohydrate and protein metabolism (sugar-active compounds). Three cortical steroids have been crystallized from the blood leaving the adrenal glands. Of these, **aldosterone** was crystallized for the first time in 1953 and is by far the most active of any of the compounds obtained from the cortex; its effect is on metabolism of inorganic compounds. **Corticosterone** and **hydrocorticosterone** are regulators of metabolism of organic compounds.

Adrenal cortical salt-active hormones control the amount of sodium, chlorine, and potassium ions in the body. The importance of sodium and potassium ions in nerve and muscle conduction has been discussed. Throughout the body sodium (Na^+) and chlorine (Cl^-) ions tend to remain outside the cell membrane, and potassium (K^+) and phosphate ($HPO_4^=$) ions are localized inside the cell. These ions play important, though not entirely understood, roles in the permeability of cell membranes and in the osmotic environment of cells. If the amount of salt-active cortical hormone is inadequate, too many sodium and chlorine ions are excreted in the urine and their concentration in the blood and body fluids goes down; water is lost from the extracellular spaces. Conversely, potassium ions are retained in the abnormal amounts. These effects result from atypical behavior of the renal tubule.

Cortical hormone promotes the reabsorption of sodium ions and inhibits reabsorption of potassium ions.

The general effect of the sugar-active hormones of the adrenal cortex, tested in experimental animals, is to raise the blood-sugar level. This is accomplished by promoting the transformation of amino acids to glucose; this glucose can be stored as glycogen, especially in the liver. The details of this phenomenon have not been elucidated.

Some of the steroid compounds recovered from adrenal cortical extracts produce effects similar to those produced by the sex hormones. Under abnormal conditions, these substances, especially the one resembling the male sex hormone, are released to the blood. This sometimes results in precocious sexual maturity in young boys and in unusual hairiness in women.

Cortical steroids have at least one other regulatory effect highly important in the arsenal of protective devices which have accumulated during the evolution of vertebrates. The release of lymphocytes from the lymphatic organs and their disruption with the liberation of gamma globulin (p. 64) appears to be regulated by cortical hormone.

Few of the endocrine glands are necessary for the continuation of life; they regulate processes that continue in their absence. Vertebrates survive removal of the hypophysis, thyroid, islands of Langerhans, and adrenal medulla, although they are far from normal when deprived of these organs. The adrenal cortex is, however, essential for life; its removal from experimental animals or its destruction by disease (Addison's disease) is always fatal unless cortical salt-active products are administered. It is also a bulwark in the struggle to maintain a relatively constant internal environment in the face of the numerous stresses or tensions to which man is subject in the modern world. Medical use of cortical hormones or of ACTH, which triggers their release from the cortex, is widespread. When it is recalled that release of ACTH is apparently stimulated by epinephrine, which is so responsive to changes in emotional state, the importance of the adrenal cortex is obvious.

The functions of the gonads in both sexes are regulated by endocrines and, in turn, the gonads produce steroid hormones which regulate the responses of other organs related to reproduction. The gonadotropic hormones of the adenohypophysis are three in number: the **follicle-stimulating hormone** (FSH), the **luteinizing hormone** (LH), and the **luteotropic hormone.**

The **testis** requires FSH in order for the male germ cells to differentiate. Elaboration of the male sex hormone, **testosterone,** occurs in the testis under the influence of LH. Testosterone conditions the differentiation of the accessory glands of the male reproductive system (p. 130) as well as the secondary sex characters, such as the comb and wattles of roosters, and the nerve reaction patterns of sex drive and pugnaciousness.

The growth of the **follicle** which surrounds the egg cell in the **ovary** is stimulated by FSH (Fig. 4.26). In mammals, the follicle becomes many-layered and its cells remain functional after the egg is shed. As the follicle reaches its full size, the ovary begins to respond to LH. A secretion known

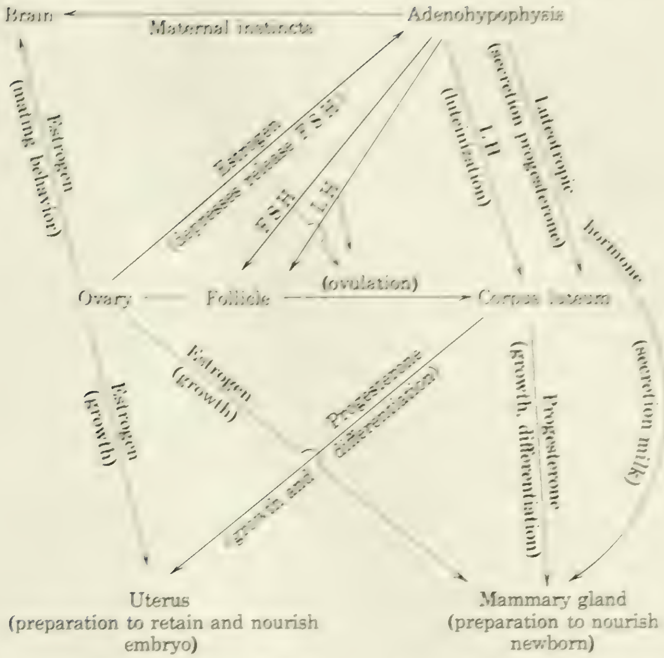
Brain
Maternal instincts
Adenohypophysis
Estrogen
(mating behavior)
Estrogen
(depresses release FSH)
FSH
LH
LH
(luteinization)
Luteotropic
(secretion progesterone)
hormone
Ovary
Follicle
(ovulation)
Corpus luteum
Estrogen
(growth)
Estrogen
(growth)
Progesterone
(growth and differentiation)
Progesterone
(growth, differentiation)
(secretion milk)
Uterus
(preparation to retain and nourish embryo)
Mammary gland
(preparation to nourish newborn)

Fig. 4.26. Hormonal regulation of reproduction in mammals.

as an **estrogen** is released, and the cells of the mature follicle become luteinized and form a **corpus luteum** after ovulation occurs. The luteinized cells respond to the luteotropic hormone and secrete **progesterone**. As soon as estrogen reaches a certain level in the blood, the adenohypophysis is depressed by it with respect to the release of FSH. This means that the stimulus to growth of follicles and subsequent formation of corpora lutea is cyclical.

Estrogen and progesterone cooperate in the synchronization of events leading to fertilization, pregnancy, parturition, and the nourishment of the newborn. In placental mammals, other than primates (p. 579), there are periodic intervals during which the female will copulate with the male. The modification of behavior pattern which makes fertilization possible is regulated by the response of the central nervous system to estrogen at the time of ovulation. Under the influence first of estrogen, followed by progesterone, the blood supply of the uterus is greatly increased. Its epithelial lining and muscular wall (see Fig. 5.2, p. 130) become much thicker and the uterine glands differentiate. By the time the fertilized egg has traversed the Fallopian tube to reach the uterus, this organ has responded to the sequential influences of estrogen and progesterone. Its wall is ready for implantation of the embryo and differentiation of the placenta (p. 163). If fertilization occurs, the hypophysis continues to secrete luteotropin and so the corpus luteum is maintained as an endocrine organ. In most mammals the maintenance of pregnancy, that is, the function of the placenta, depends on the progesterone released by the corpus luteum. In others, including man, the chorionic portion of the placenta becomes an endocrine organ secreting a gonadotropic hormone in addition to progesterone. This origin of a new site for the production of progesterone makes possible an extended period of gestation resulting in the birth of more fully developed young. Birth is correlated with a reduction in the amount of progesterone released to the blood.

Some estrogen is secreted during pregnancy, and it stimulates growth in the mammary glands. After growth has occurred, the glands differentiate their secretion under the influence of progesterone. At the time of parturition, the mammary glands become responsive to the luteotropic hormone and milk becomes available for the suckling newborn. Changes in the behavior pattern are also conditioned by the luteotropic hormone which releases, so to speak, the nesting and maternal instincts of the expectant mother.

This sequence of events so beautifully coordinated by hormonal and central nervous mechanisms insures the continuity of the species. Insofar as the reactions of the reproductive tract are concerned, the effect of the ovarian hormones is on fundamental metabolic processes. The first responses of the uterus to estrogen are an increase in vascular bed and enhanced permeability of capillaries together with a rise in oxygen consumption. Then there occurs a marked shift of water and ions to the uterine wall. Utilization of glucose increases and, next, synthesis of new protoplasm followed by increased cell division. Growth of the uterus has occurred. How do these particular steroid molecules set in train these adaptive processes? Since the molecules are believed to be too large to enter the cell, current hypotheses assume that the initial response occurs at the cell membrane. The final elucidation awaits further research, perhaps new methods.

Regulation of Breathing and Body Temperature. We have seen in the special events of reproduction how several interrelated factors regulate the sequences in an adaptive fashion. This is equally impressive in continuous regulations of vital functions such as breathing and, in warm-blooded animals, maintenance of a constant body temperature.

The regulatory mechanisms for the control of breathing are conditioned by the amount of carbon dioxide in the blood. In higher vertebrates, ventilation of the lungs occurs as a result of contraction of thoracic muscles aided, in mammals, by the diaphragm. The rhythmicity of the respiratory movements is a reflection of the rhythmic activity of the cells of the respiratory centers located in the medulla of the brain. These cells are very sensitive to minute changes in the amount of carbon dioxide in the blood flowing through the capillaries about them. A slight elevation in the carbon dioxide tension stimulates the cells of the respiratory centers, and impulses are established which are finally conducted along the thoracic spinal nerves to the muscles between the ribs; contraction of these muscles pulls air into the lungs. As the lungs fill, tension builds up in their walls and nerve impulses are established. These bring about inhibition of the muscular movements of inhalation, allowing the lungs to collapse. Ventilation of the lungs lowers the carbon dioxide tension in the blood. When it builds up again, the respiratory centers are stimulated again. This basic rhythm of quiet breathing is modified during exercise, which increases the amount of carbon dioxide in the blood and so accelerates breathing. The respiratory center can also be stimulated by emotional reactions such as fear. And man can voluntarily increase the rate of breathing or hold his breath for limited periods.

The body temperature of warm-blooded animals is not really constant, or uniform in all regions. In man, for example, the temperature of the mouth cavity normally ranges from 97.7°F. to 99.5°F. with an average of 98.6°F. The temperature of the rectum averages about 1°F. higher and that of the skin of the axilla about 1°F. lower. Temperatures on exposed portions of the skin average 4° to 9°F. lower than internal temperatures. The temperature of the internal organs is, however, regulated within narrow limits. The rate of chemical reactions is very sensitive to temperature changes, and the smooth flow of metabolic processes depends on the maintenance of an optimal temperature. Catabolic reactions of metabolism, especially in the liver, and muscle contractions are constantly tending to increase the body temperature, since during the transformation of energy much is diverted to heat. Blood in the internal capillaries has its temperature raised, and distribution of heat is one of the functions of the circulatory system. The maintenance of a constant temperature under these circumstances requires that heat be lost under optimal environmental conditions.

Heat is lost by conduction from the blood in the capillaries of the skin to the surface of the body, from which it moves to the surrounding medium, whether air or water. Cooling also occurs as a result of evaporation of water lost through sweat glands and the lungs. The temperature of the surrounding medium influences the rate of heat loss; the cooler the environment, the more rapid the loss of body heat.

If the internal blood temperature rises, the hypothalamic centers for heat control are activated. Impulses flowing over sympathetic nerves bring about dilatation of the cutaneous blood vessels and an increase in cardiac output—more blood passes through the cooling area. The release of secretion by the sweat glands is also stimulated by way of the autonomic nerves. Evaporation of sweat cools the surface of the skin and increases the loss of heat from the blood. Animals which lack sweat glands exhibit increased ventilation of the lungs or panting; this increases the rate of evaporation from the air passages.

When the environmental temperature is elevated, conscious controls contribute to heat loss. Animals seek out cooler parts of their environment, expose as much body surface as possible, and become relatively inactive, decreasing heat production. Man reduces his clothing, moves the air about him more rapidly by means of fans in order to increase the rate of evaporation, eats less, and works as little as possible when summer temperatures are extreme.

It is necessary for warm-blooded animals to conserve their heat when the external temperature drops. Autonomic nervous regulation produces constriction of peripheral blood vessels. Voluntary regulation is through reduction of exposed body surface by huddling and finding additional protection in nests or sheltered places, seeking of warmer climes by migrating animals, heavier clothing and artificial heat for man. Heat production is raised by increased intake of food, utilization of fat stores, and involuntary muscular activity or shivering. Elevation of the hair in fur-bearing mammals conserves heat, but piloerection in man only produces "gooseflesh."

Hormones play a part in temperature regulation. The secretion of the thyroid regulates cellular oxidation, an important source of body heat; the basal metabolic rate is normally higher in cold weather. Epinephrine increases the availability of glucose, a major source of energy and heat. Adrenal cortical salt-active hormone controls the concentration of the blood, thus affecting its rate of flow; a more concentrated blood conserves heat because it flows more slowly.

Fever is, in effect, the result of conservation of body heat when it is physiologically unnecessary. Something goes wrong at the thermoregulatory centers in the hypothalamus, but exactly what happens is not known.

Summary

The material discussed in this chapter has been selected to acquaint you with the ways in which coordination is accomplished in vertebrates. In the complex adjustments of the internal environment of the cells and of the animal as a whole to its external environment, there is a delicately balanced interplay of autonomic nervous and hormonal mechanisms, modified by the emotions and conscious nervous control. Similarly, we find the several mechanisms of integration working together in the coordination of the events leading to parenthood: growth and differentiation of the germ cells, behavior patterns in male and female that lead to fertilization of the egg cell and, in many vertebrates, to its incubation and to the care and feeding of the young after hatching or birth. Regulation of intrauterine gestation in placental mammals appears to be entirely hormonal.

The life of the individual is maintained as a result of the distinctive protoplasmic capacities of metabolism and responsiveness. The life or continuity of the species depends on the capacity of reproduction, the implications of which we must now examine.

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CHAPTER 5

REPRODUCTION AND DEVELOPMENT IN CHORDATES[1]

CHAPTER 5

Living organisms are distinguished by the capacities of metabolism, responsiveness, and reproduction. The primary effect of the activities of the organ systems that are specialized to provide the metabolic requirements of cells and to coordinate the functions of all parts of the organism is to maintain the life of the individual. The individual also exists as the potential parent of a new generation of his species. As a result of the capacity of reproduction certain cells can become detached and, either alone or after union with cells of another organism of the same kind, can give rise to a new individual capable of becoming like the parent or parents in all essential respects. Reproduction, like metabolism and responsiveness, is dependent on a cellular mechanism, and a specialized organ system is related to this activity of the individual.

The Reproductive System

The reproductive system of vertebrates consists of the **reproductive organs**, or **gonads**, in which the germ cells become differentiated, and the **reproductive ducts**, through which the germ cells leave the body. During the development of the individual, the reproductive and urinary systems arise in close association, so that structurally they form what is known as the urinogenital system (p. 57). The functions of the two parts of this system are entirely

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[1] The group of animals called the chordates includes the vertebrates and their near relatives (p. 217).

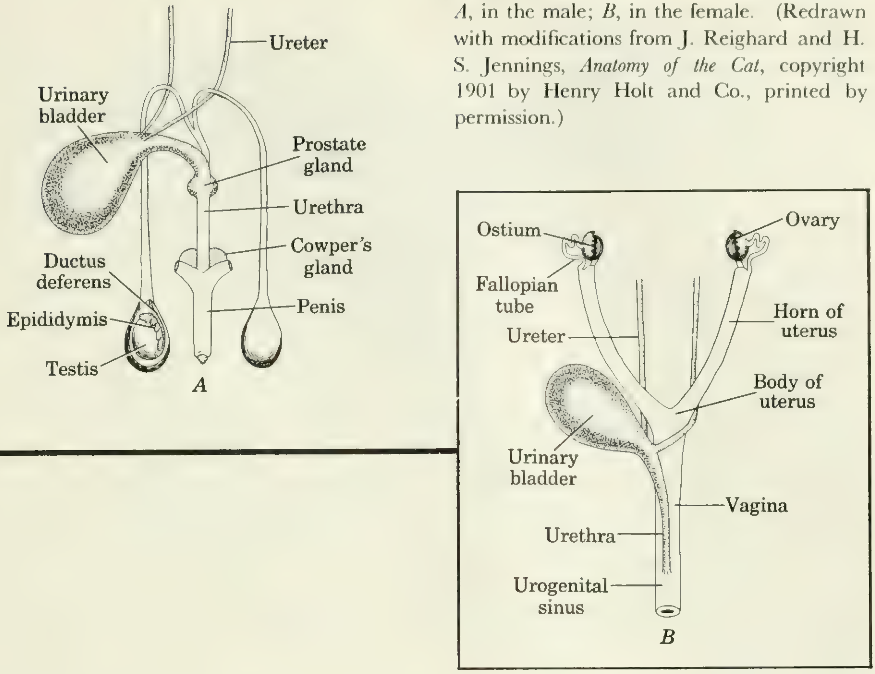

Ureter
Urinary bladder
Prostate gland
Urethra
Ductus deferens
Cowper's gland
Epididymis
Penis
Testis
A
Ostium
Ovary
Fallopian tube
Ureter
Horn of uterus
Body of uterus
Urinary bladder
Vagina
Urethra
Urogenital sinus
B

Fig. 5.1. The reproductive system of the cat. *A*, in the male; *B*, in the female. (Redrawn with modifications from J. Reighard and H. S. Jennings, *Anatomy of the Cat*, copyright 1901 by Henry Holt and Co., printed by permission.)

unrelated, and we shall be concerned here with only the reproductive or genital system. In the vertebrates, as in the majority of animals, there are typically two sexes; individuals are either male or female (p. 208). Both gonads and ducts differ in the male and female reproductive systems.

In male fishes and frogs the two gonads, or **testes**, are suspended by mesenteries, the **mesorchia**, from the dorsal surface of the pleuroperitoneal cavity ventral to the excretory organs which are mesonephroi (p. 57). In reptiles and birds the testes are suspended near the metanephroi, or kidneys, but in male mammals the gonads are located posterior to the kidneys and in many species descend until they lie outside the peritoneal cavity in the scrotum. The testis is essentially a mass of small **seminiferous tubules**, along the walls of which the primordial germ cells are found (p. 133). At the time of sexual maturity, numerous spermatozoa fill the cavities of the seminiferous tubules, which are continuous with the reproductive ducts. The fishes and frogs have numerous small ducts, the **ductus efferentes** (vasa efferentia), which are continuous with the seminiferous tubules in the testis and also with the excretory tubules. In such animals spermatozoa pass from the tubules of each testis to the ductus efferentes, which are located in the mesorchium, and into the excretory tubules. Thence, the path to the outside is by way of the excretory duct and cloaca, and the male germ cells are shed from the body through the anus. In reptiles, birds, and mammals, the spermatozoa no longer pass through the excretory organs but leave each testis through a coiled duct, the **epididymis**. This is continuous with a **ductus deferens** (vas

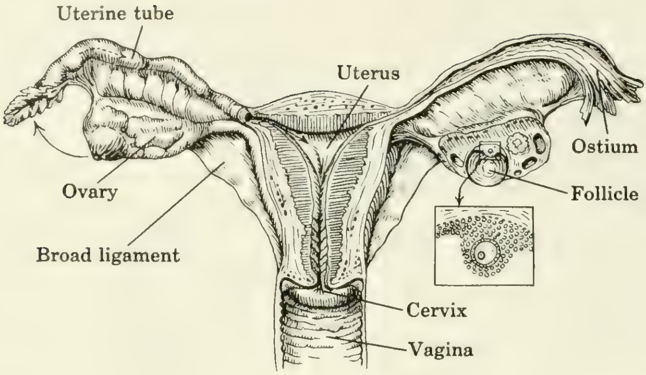


Fig. 5.2. Diagram of ovaries and reproductive tract in man; the uterus and right Fallopian tube are shown with their walls cut away to reveal their cavities, and the ostium is pulled away from the ovary which is shown in section. On the left, arrows indicate the path of the egg from ovary to uterus; this figure is about one-half natural size. A part of a mature follicle with its egg or ovum is shown in the inset. (Redrawn from G. W. Corner, *Ourselves Unborn*, copyright 1944 by Yale University Press, printed by permission.)

deferens) which opens into the ventral part of the cloaca in reptiles and birds and into the **urethra**, or neck of the urinary bladder, in mammals (Fig. 5.1*A*; cf. Fig. 3.11, p. 57). There are three kinds of so-called **accessory glands** which secrete constituents of the seminal fluid into the ductus deferens in mammals.

The female reproductive organs are known as **ovaries** (Fig. 5.1*B*). They are suspended by ovarian mesenteries, the **mesovaria**, ventral to the anterior end of the excretory organs in vertebrates other than the mammals; a descent of the ovaries into the pelvic region of the peritoneal cavity occurs in mammals (see Fig. 4.8, p. 94). Ovaries may be sac-like, as they are in the frog, or solid, as they are in higher vertebrates (Figs. 5.2 and 5.4*A*). The wall of an ovary of the frog and the outer layer of an ovary of a mammal are composed, for the most part, of relatively undifferentiated germ cells, each surrounded by an envelope of cells, the **follicle** (Fig. 5.3*B* and p. 122). In those vertebrates in which the oöcyte stores a large amount of food material, the follicle consists of only two or three layers of cells and becomes very inconspicuous as the growth of the oöcyte is completed. Contrasted with such a condition is the great growth of the follicle in mammals in which little food is stored in the oöcyte. The mammalian follicle becomes vesicular, and its cavity is filled with follicular fluid.

The reproductive ducts of the female are the **oviducts**, which are not directly continuous with the ovaries but open into the coelomic cavity. The **ostium**, or opening of the oviduct, is located in the anterior end of the coelom in the frog but lies nearer the ovary in higher vertebrates. In many mammals the ostium practically surrounds the ovary (Fig. 5.2). When **ovulation**, or rupture of the follicles, occurs in the frog, the eggs are discharged from the ovary and drop into the coelom, where they are carried through the ostia of the oviducts by the beating of cilia. In higher forms the eggs pass directly into the ostia as ovulation occurs and are present in the coelom only under atypical conditions.

Attention may be called here to the several meanings which the word egg has. We speak of birds' and reptiles' eggs, which most often have been fertilized and are in the process of development, and which contain albuminous envelopes in addition to the female germ cell (Fig. 5.4*B*). We refer to ovarian eggs when we mean the growing oöcytes, and to tubal eggs when we mean recently ovulated female germ cells which may be either oöcytes or ova (p. 139) or may be fertilized and in the early stages of development. The student should not be confused by the several uses of this word, which are so widely accepted that it would be impossible to change them. Wherever clarity demands it, a more restricted term will be used; in other cases, the meaning will be clear from the context.

The frog has a relatively unspecialized oviduct. Jelly is secreted by the cells lining the long coiled portion, and the eggs may be stored temporarily in the expanded ovisac which opens into the cloaca, through which the eggs pass to the outside by way of the anus. The albumen, or so-called white, of a reptile's or bird's egg is secreted by a specialized region of the oviduct; the egg envelopes and shell are secreted by different regions. Animals that lay eggs which are well supplied with food and in which the young develop outside the body are known as **oviparous.** Among the fishes and reptiles some forms retain the fertilized eggs in a uterine portion of the oviducts during development. In such species the young are nourished by the food stored in the egg, and these forms are referred to as **ovoviviparous.** A few of the most primitive mammals, such as *Ornithorhynchus*, the duckbill (see Fig. 18.30*A*, p. 581), lay eggs and have paired oviducts like those of

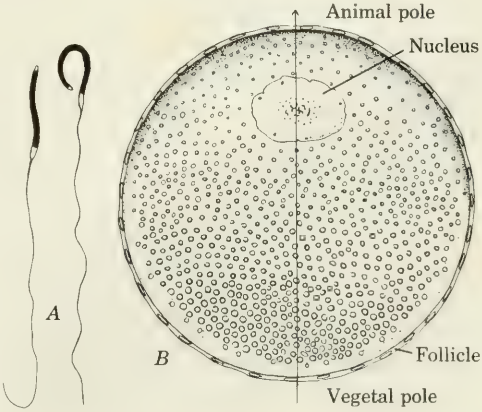


Fig. 5.3. Germ cells of the frog, showing difference in size. *A*, mature spermatozoa: ×1070. *B*, an oöcyte, with its follicle, at the end of the growth period: ×30; drawn in section to show the unequal distribution of yolk in the animal and vegetal hemispheres and the location of the nucleus in the animal hemisphere; the arrow indicates the egg axis.

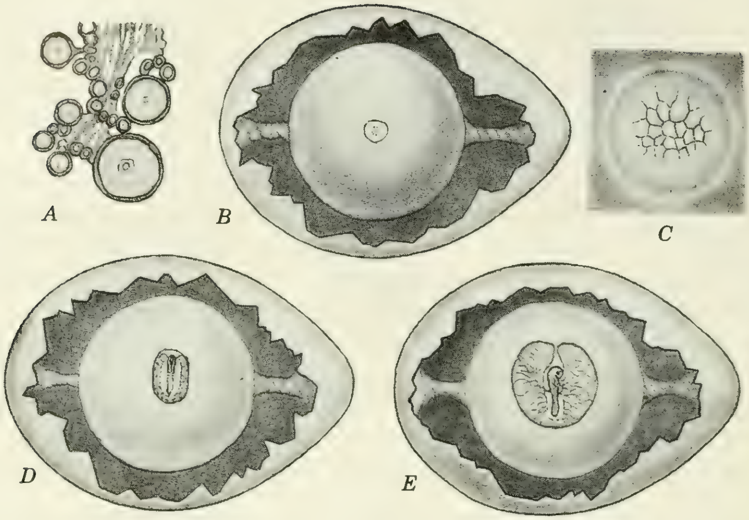
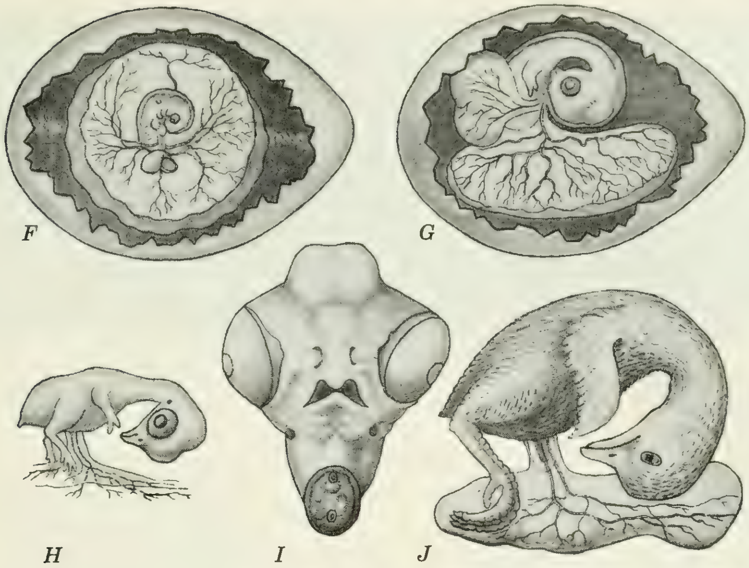


Fig. 5.4. The development of the hen's egg. *A*, portion of the ovary, showing oöcytes in different stages of growth. *B*, the egg at the time of laying, with part of the shell removed to show the yolky zygote (the "yolk") suspended by denser cords of albumen (the "white"); the small disk of cytoplasm called the blastodisk is shown on the surface of the zygote. *C*, the blastodisk removed from the egg, to show its cleavage; after cleavage it is called the blastoderm. *D–G*, successive stages in the origin of the embryo and the spread of the margin

reptiles. Other mammals retain the fertilized eggs during development, and the oviducts exhibit conspicuous modifications related to retention and nourishment of the embryo or developing young individual. These mammals are **viviparous.** The ostial portion of each oviduct is slender and is known as the **Fallopian tube,** or **uterine tube** (Fig. 5.1*B*). Posterior to the Fallopian tube, the oviduct expands to form the **uterus,** which is the region where the embryos develop, and terminates in a short **vagina,** which opens into the urogenital sinus. Although primitive mammals have a pair of oviducts, in higher forms there is a progressive fusion beginning with the vaginal portions, and in man the Fallopian tubes are the only paired parts (Fig. 5.5).

Vertebrates are typically either male or female, but they pass through a developmental stage in which they are sexually indifferent; that is, it is impossible at such a stage to determine whether the primordial gonads are ovaries or testes, and the primordial reproductive ducts of both sexes are present. During later development the gonads differentiate into either ovaries or testes; the correlated ducts develop, and those of the opposite sex degenerate. In the adult males of some fishes and frogs, however, the oviducts



of the blastoderm to form the yolk sac, in which blood vessels soon appear. The amnion has been formed in *F* and *G* but it is difficult to distinguish; in *F* the small sac at the posterior end is the allantois, which is also seen in *G* as the smaller of the two appended sacs. *H* and *J*, later embryos removed from their shells, with the amnion and allantois removed; only the yolk stalk remains in *H*, and the yolk sac is shown in *J*. *I*, the head of an embryo removed and viewed from the front, showing mouth, sense organs, and remains of the gill furrows. (Redrawn from M. Duval, *Atlas d'embryologie*, 1889.)

persist as rudimentary, non-functional organs, vestiges of the indifferent period of development.

Differentiation of the Germ Cells

The somatic cells are divisible into groups on the basis of characteristic features of the structure of their cytosomes (pp. 58–69). These cells are specialized, or differentiated, to perform certain functions related to the maintenance of the life of the individual. There are other cells, the **germ cells,** which become differentiated in connection with the capacity of reproduction, as a result of which continuity of the species is assured. In other words, new individuals arise from the germ cells of previously existing individuals.

It has been stated that cells arise by division of previously existing cells, and this statement is true of the germ cells as well as of the somatic cells. The primordial germ cells arise, of course, from the same ancestor that gives rise to

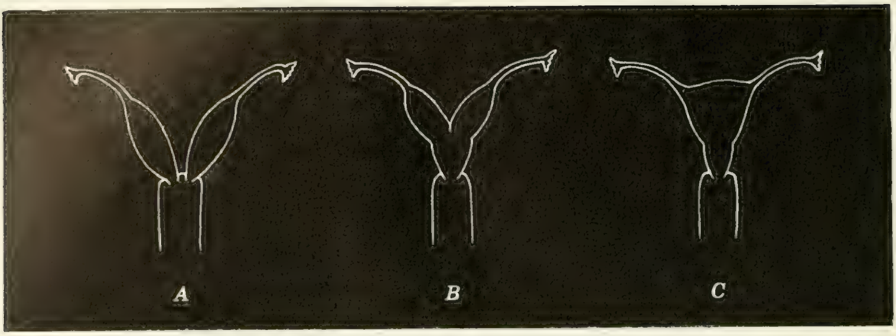


Fig. 5.5. The oviducts of mammals, showing progressive fusion of uterine portions. *A*, duplex uterus, as in rabbits; *B*, bicornuate uterus, as in swine; and *C*, simplex uterus, as in man.

all the somatic cells, that is, from the zygote, the single cell from which the entire organism develops (p. 145). In some animals it is possible to trace through successive cell divisions the history of the germ cells, which may be set aside at a very early stage of development (Fig. 5.6). During the time when the somatic cells are increasing in number and becoming specialized, the potential germ cells become localized in the reproductive organs in an undifferentiated condition. Usually rounded, the cytosome is relatively small in comparison with the nucleus. There is little activity until the animal nears the age of sexual maturity.

Specialization of the germ cells, or **gametes**, occurs in vertebrates during the process of **gametogenesis**, or **maturation**. The maturation or differentiation of a male germ cell is **spermatogenesis**, the origin of the spermatozoon, or sperm; maturation of a female germ cell is **oögenesis**, the origin of the ovum, or egg.

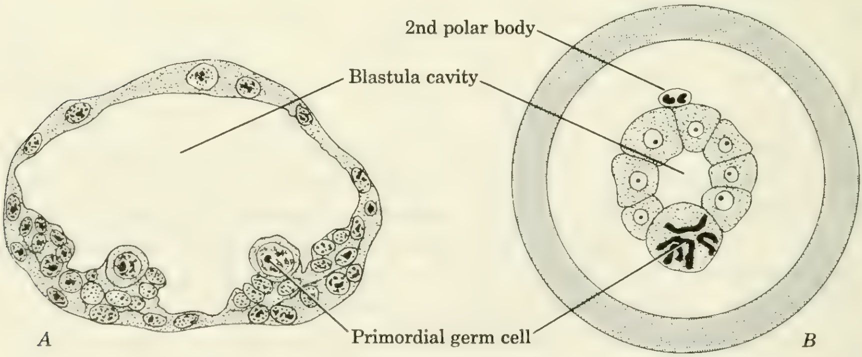


Fig. 5.6. Origin of primordial germ cells. *A*, section of a late blastula stage in the development of a mollusk, *Sphaerium striatinum:* ×265. *B*, section of a blastula stage (32 cells) of a roundworm, *Parascaris equorum* (*Ascaris megalocephala bivalens*): ×710. (*A*, from F. H. Woods, 1931, *Journal of Morphology and Physiology*, vol. 51.)

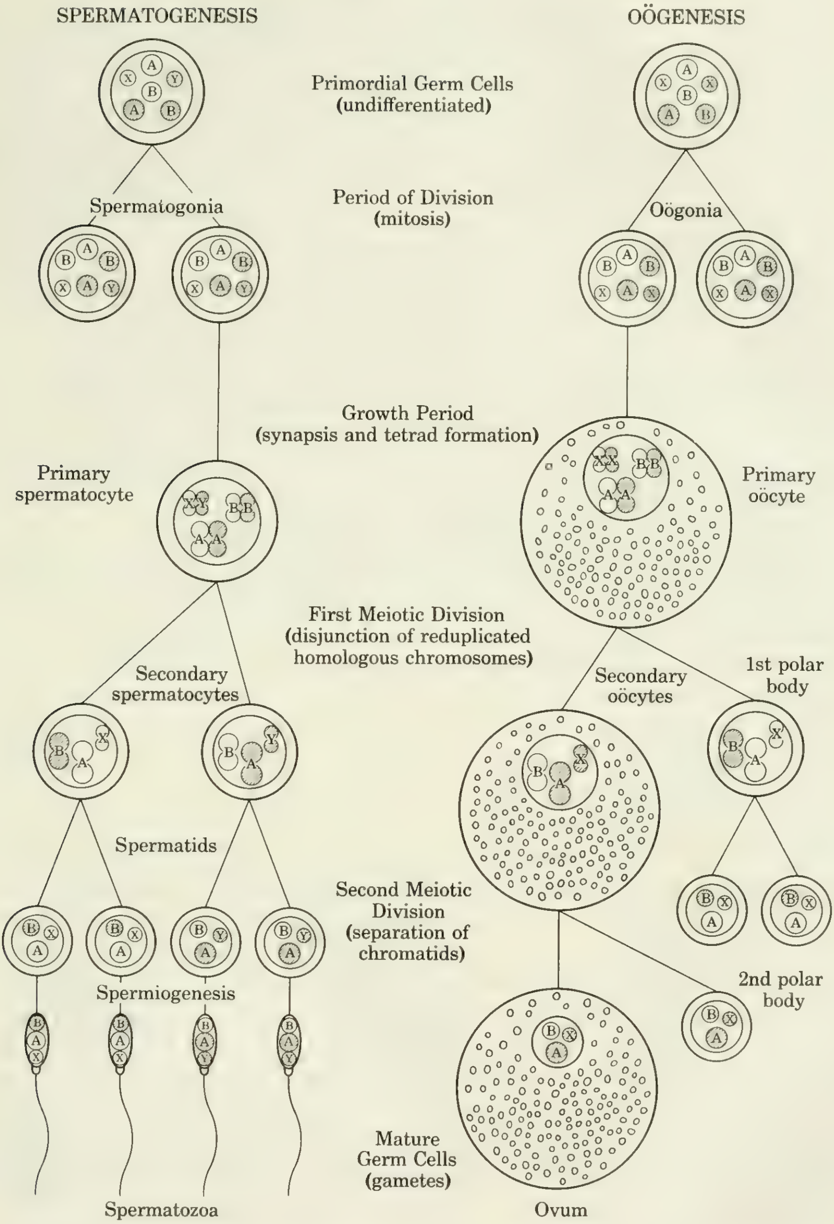

SPERMATOGENESIS
OÖGENESIS
Primordial Germ Cells
(undifferentiated)
Spermatogonia
Period of Division
(mitosis)
Oögonia
Growth Period
(synapsis and tetrad formation)
Primary
spermatocyte
Primary
oöcyte
First Meiotic Division
(disjunction of reduplicated
homologous chromosomes)
Secondary
spermatocytes
Secondary
oöcytes
1st polar
body
Spermatids
Second Meiotic
Division
(separation of
chromatids)
2nd polar
body
Spermiogenesis
Mature
Germ Cells
(gametes)
Spermatozoa
Ovum

Fig. 5.7. Gametogenesis in animals; diagrammatic. Homologous chromosomes are lettered alike; A and B are autosomes, X and Y are sex chromosomes. The chromosomes shown in black represent the paternal contribution; the unshaded ones are maternal in origin (p. 142). During the growth period food is stored in the cytosome of the primary oöcyte; this yolk remains in the ovum and is not distributed to the polocytes.

During gametogenesis the cytosome undergoes modifications that differ in male and female germ cells and that result in the formation of a male gamete smaller than the female gamete. Gametes of different sizes are known as **anisogametes** (Fig. 5.3) in contrast to the **isogametes** found in some of the unicellular animals (p. 267). The nuclear changes in gametogenesis are closely comparable in both types and constitute the process of **meiosis.** In other words, meiosis is the term applied to the distinctive nuclear phenomena that occur during the maturation of the germ cells of vertebrates and other animals. The essential characteristic of meiosis is that it results in the distribution to each mature germ cell of only one chromosome from each of the pairs of homologous chromosomes present in the primordial germ cells of an organism. Consequently, each mature germ cell has only half as many chromosomes as the somatic cells and the primordial germ cells had; these chromosomes are unpaired, and the number present constitutes the **haploid number** of the species (see Fig. 2.12*C*, p. 42). This fact is very significant in the light of the activities of the germ cells and the relation of the chromosomes to the hereditary determiners.

If we consider the process of spermatogenesis, we find numerous undifferentiated germ cells, known as **spermatogonia,** in the testes (Fig. 5.7). Spermatogonia give rise to other spermatogonia by the process of mitosis during the **period of division.** When any spermatogonium is ready to begin its differentiation, it enters the **growth period,** during which there is some increase in the size of the cytosome and synapsis occurs in the nucleus. The chromosomes of a spermatogonium occur in pairs of similar size and shape with the exception of the X-chromosome; this either occurs alone or has a companion Y-chromosome, which may not be the same size or shape (see Fig. 2.12*E*, p. 42). During the growth period the homologous chromosomes come to lie side by side in pairs, a phenomenon known as **synapsis.** The chromosomes at this stage are comparable to the prophase threads of mitosis. As they shorten and thicken, it is seen that each member of a pair is double in a way that is comparable to a metaphase chromosome during mitosis. Thus, each "pair" of chromosomes is really a group of four half-chromosomes, or **chromatids,** and for that reason is called a **tetrad** (Fig. 5.9*B*). There are half as many tetrads as there were chromosomes, one tetrad for each pair of homologous chromosomes. The cell is now known as a **primary spermatocyte.** A spindle appears in this cell, and the tetrads become arranged at the equatorial plate. It can be observed that the two chromatids derived by duplication from a single chromosome are connected by its kinetochore. At anaphase, the two kinetochores of a tetrad separate toward opposite poles of the spindle; that is, the two chromatids derived by duplication from a single chromosome and known as a **dyad** pass to one pole, and the two chromatids derived by duplication from its synaptic mate pass to the opposite pole. This is known as the **first meiotic** or **first maturation division;** it is the **disjunctional division** because the two homologous chromosomes which had been paired are now separated, or disjoined, in such a way that they pass to separate cells. The cells arising from the division of the primary spermatocyte are **secondary spermatocytes;** they begin the **second meiotic** or **second maturation division** almost immediately. A spindle is formed, and the sister half-chromosomes (dyads) become arranged at the equatorial plate. After replication of the kinetochore, separation occurs during the anaphase in such a way that the two chromatids of each chromosome pass to opposite poles of the spindle. This is the **equational division** and is entirely comparable with any mitotic division, except that only half the typical number of chromosomes is present in the cell. The two cells formed by the division of each secondary spermatocyte are the **spermatids.** Four spermatids arise from each primary spermatocyte, and each one contains one chromatid of the four which are formed by duplication of the members of each pair of homologous chromosomes.

Cytosomal differentiation of the spermatids occurs next; this is known as **spermiogenesis** (Fig. 5.8). The essential changes consist in the outgrowth of a vibratile flagellum from one of the centrioles of the spermatid and the loss of most of the cytoplasm. The nucleus becomes condensed and is surrounded by a very thin layer of cytoplasm in the **head** of the mature **spermatozoon.** The centrioles and a small mass of cytoplasm form the **middle piece,** and the third part is the **tail** surrounding the flagellum, by means of which the mature male germ cell, or **microgamete,** is able to swim (Fig. 5.3*A*). The spermato-

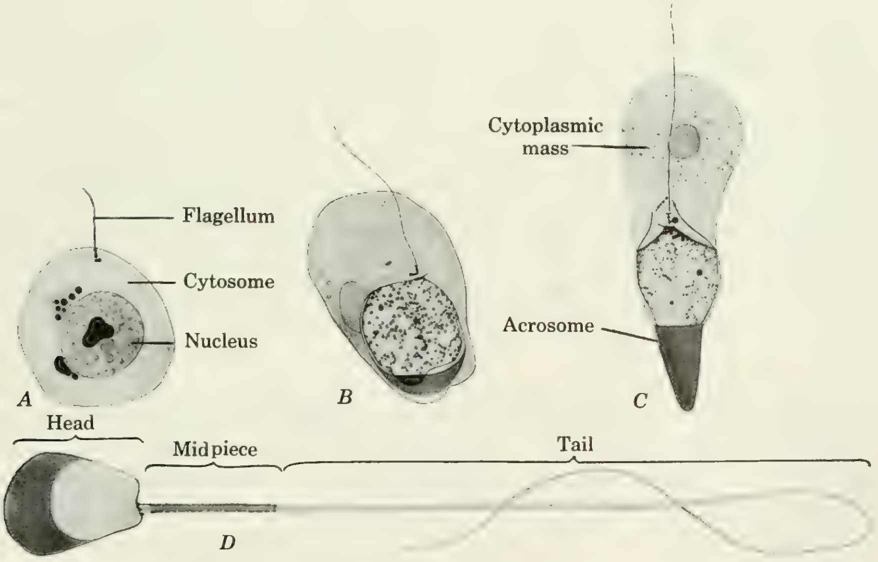


Fig. 5.8. Stages in spermiogenesis in the guinea pig. *A*, spermatid with early growth of flagellum from one centriole. *B* and *C*, showing the centrioles near the nucleus, the accumulation of cytoplasm along the flagellum, and the formation of the acrosome, which is the most anterior part of the spermatozoon. *D*, mature sperm, showing head, midpiece, and tail; the cytoplasmic mass has been detached and lost. (From F. Meves, 1898, *Archiv für mikroscopische Anatomie*, vol. 54.)

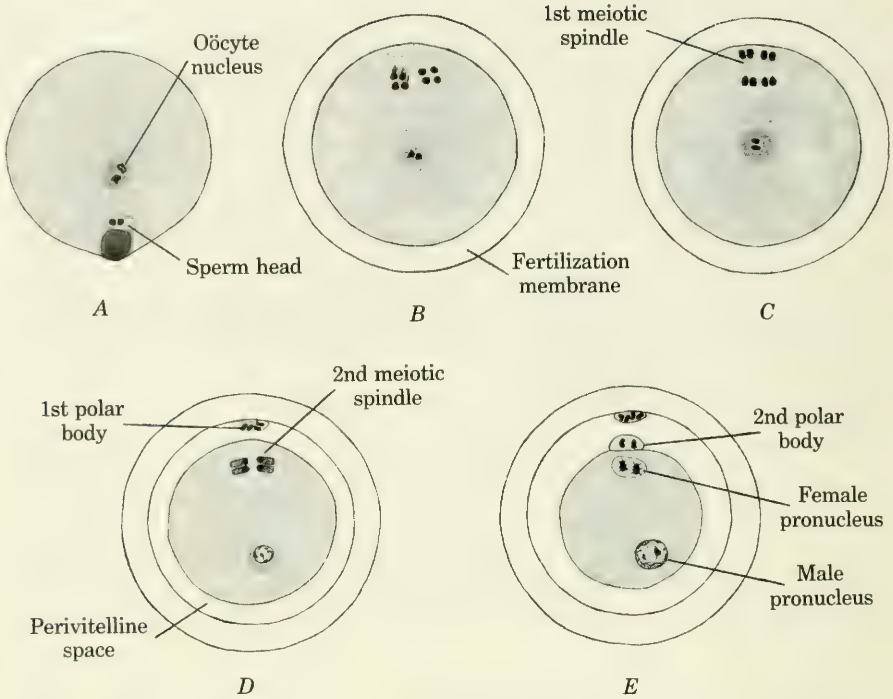


Fig. 5.9. Meiosis during oögenesis of a roundworm, *Parascaris equorum* (*Ascaris megalocephala bivalens*). *A*, a primary oöcyte into which a sperm carrying the haploid number of chromosomes (two) has just penetrated. *B*, showing two tetrads, each containing four half-chromosomes (chromatids), on the equatorial plate of the spindle of the first meiotic division. *C*, showing the anaphase of the first meiotic division with two chromatids from each tetrad passing to each end of the spindle. *D*, showing the two pairs of chromatids on the spindle of the second meiotic division. *E*, showing the nucleus of the mature female germ cell (female pronucleus), the first and second polar bodies, and the nucleus of the sperm head (male pronucleus), which has been inactive since its entrance. The meiotic spindles in *Parascaris* do not have centrioles or astral rays. A perivitelline space is formed between the oöcyte and the fertilization membrane which arises after the sperm enters. All figures ×690.

zoon is specialized for motility and contains one-half as many chromosomes as the primordial germ cells and somatic cells contain, one chromosome corresponding to each of their pairs. Four functional spermatozoa are derived from each primary spermatocyte.

The process of oögenesis, or maturation of the female germ cell, is entirely comparable to that of spermatogenesis insofar as nuclear changes are concerned; the cytosomal specialization differs (Figs. 5.7 and 5.9). The undifferentiated germ cells found in the ovaries are known as **oögonia** and give rise to other oögonia during the **period of division.** Each of these presently enters its **period of growth,** and the homologous chromosomes pair in synapsis and become duplicated to form tetrads. This is the time when cytosomal differentiation occurs in the female germ cell, or **primary oöcyte,** as it is now called. In all female vertebrates certain of the undifferentiated germ cells form a layer around the primary oöcyte. This envelope, or **follicle,** serves a nutritive function during the storage of food, usually in the form of yolk, which occurs in the oöcyte during the growth period. The follicles of different vertebrates vary in thickness; those of mammals are very large (Fig. 5.2 and 5.3*B*). Not all vertebrates store a large supply of food for the young animal that may develop from the egg if it is fertilized. The method and place of development are correlated with the amount of food stored in the female germ cell and will be discussed later. When food storage is complete, the primary oöcyte divides to form two cells very unequal in size. There is a large cell, the **secondary oöcyte,** containing most of the food, and a very small cell, the **first polar body,** which has only a thin layer of cytoplasm around its nucleus. The division which produces these cells is the **first meiotic** or **disjunctional division,** and the nucleus in each cell contains half-tetrads, or dyads, just as does the nucleus of each of the secondary spermatocytes. At the **second meiotic** or **equational division** the first polar body divides to form two polocytes, or polar cells, of equal size, but the secondary oöcyte gives rise to a small cell, the **second polar body,** and to the **ovum,** or mature female germ cell, which contains most of the food that was stored in the primary oöcyte. The three polar cells and the ovum have comparable nuclei; each contains one chromosome corresponding to each homologous pair in the oögonia and somatic cells. Only one ovum, or **macrogamete,** is produced from each primary oöcyte. The small polar cells are non-functional and die.

All the cells of the vertebrate organism become differentiated to perform the activities of the particular organs of which they form a part. Specialization of the germ cells occurs much later in life than differentiation of most of the somatic cells and is limited to the period of sexual activity in the organism. Primordial germ cells are totipotent cells (p. 159). The essential difference between somatic cells and the germ cells is to be referred to their activities: the somatic cells are specialized in ways which contribute to the maintenance of the life of an individual, whereas differentiated germ cells make possible the reproduction of a new individual and so provide for continuity of the species. Both groups of cells have the same essential structure of nucleus and cytosome; both have the same requirements for life. Somatic cells contribute to the existence of the germ cells of the same generation, whereas germ cells make possible the existence of somatic cells of the succeeding generation.

Reproduction

Historical. Since Aristotle's observations, in the fourth century B.C., on the developing hen's egg, students have been interested in the origin of new individuals. Before the invention of the microscope the male germ cells could

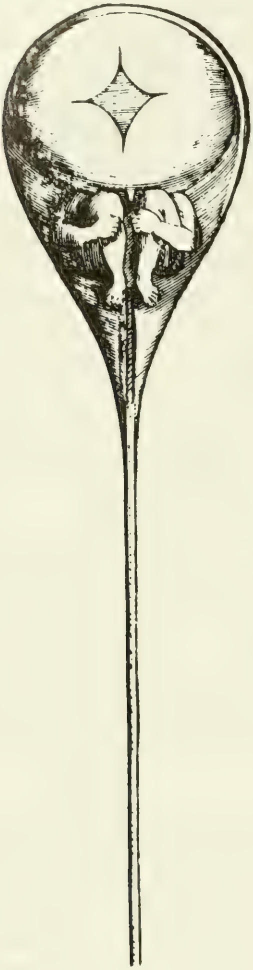


Fig. 5.10. Homunculus, as imagined to exist in the head of the spermatozoon of man. (From N. Hartsoeker, *Essay de dioptrique*, Paris, 1694.)

not be seen. Spermatozoa were studied first in 1677 by Antony van Leeuwenhoek, a Dutch microscopist. Several observers soon associated the occurrence of spermatozoa in the seminal fluid with the phenomenon of reproduction, and some workers stated that each spermatozoon contained a fully formed, miniature individual. This tiny individual was called a homunculus and was believed to grow, nourished by the female, until the time of birth (Fig. 5.10). Such a fantastic idea was opposed by other scientists of the eighteenth century who believed that new individuals were fully formed in the egg cells and that spermatozoa were parasitic in character and entirely unnecessary for reproduction. These ideas of minute individuals encased in spermatozoa or in eggs were responsible for the Theory of Preformation, according to which development was simply the growth of a small individual preformed in the so-called germ.

In 1824, Prévost and Dumas proved that spermatozoa are essential for the formation of new individuals by filtering the seminal fluid of male frogs before mixing it with eggs. No new individuals were formed under such conditions. Even this experiment did not establish the fact that the sperm and the egg united. It was not until 1875 that the actual penetration of an egg by a spermatozoon, followed by the union of the two nuclei, was observed independently by Hermann Fol and Oscar Hertwig in sea urchins (p. 499). When it is recalled that the Cell Theory was formulated in 1838 and 1839 (p. 11), the recognition by Hertwig and Fol that the spermatozoon and egg were cells is not surprising. With this recognition a sound interpretation of reproduction, which had baffled students for hundreds of years, was soon reached. The earliest workers had lacked mechanical equipment in the form of microscopes, but the improvement in lenses was not all that was needed. Progress in science is always dependent on what scientists think about the facts they observe. The conception of cells as the units of structure and function was, and is, as great a scientific tool as the microscope, and we are strikingly impressed with this fact in a study of reproduction and development.

Methods of Reproduction. Reproduction, or the formation of a new individual, is accomplished in several different ways. On the one hand, it may occur without the production of germ cells and be the result of the activity of only one individual—**asexual** or **uniparental reproduction**. On the other hand, germ cells, or **gametes**, may be produced by two individuals and unite in pairs—**sexual** or **biparental reproduction**. Among the unicellular animals asexual reproduction is brought about by **cell division** (p. 38). If this cell division produces two equal cells, it is known as **fission**; if the two cells are unequal in size, the process is called **budding**. Sometimes a process of multiple cell division or **multiple fission** occurs, with the result that many new individuals are produced at the same time (p. 245). Some of the simpler multicellular animals, such as the coelenterates, reproduce asexually by the methods of budding and strobilization; the flatworms undergo fission (pp. 281, 299, 305, and 322). Sexual reproduction occurs throughout the Animal Kingdom by the method of **syngamy**, or union of two gametes to form a **zygote**. When the gametes are differentiated into microgametes and macrogametes, the process of syngamy is known as **fertilization**. Among the protozoans both isogametes and anisogametes occur, but anisogametes are typical of multicellular animals. Syngamy usually takes place in animals that produce anisogametes, but **parthenogenesis**, or development of a macrogamete without union with a microgamete, sometimes occurs, notably among the rotifers and insects (pp. 346, 472, and 535).

Reproduction is typically a function of adult animals; germ cells are produced by mature individuals. However, in one of the amphibians, the axolotl, immature or larval animals give rise to germ cells which function in reproduction. Reproduction by immature animals is called **pedogenesis** and is known to occur in several invertebrate groups (p. 330).

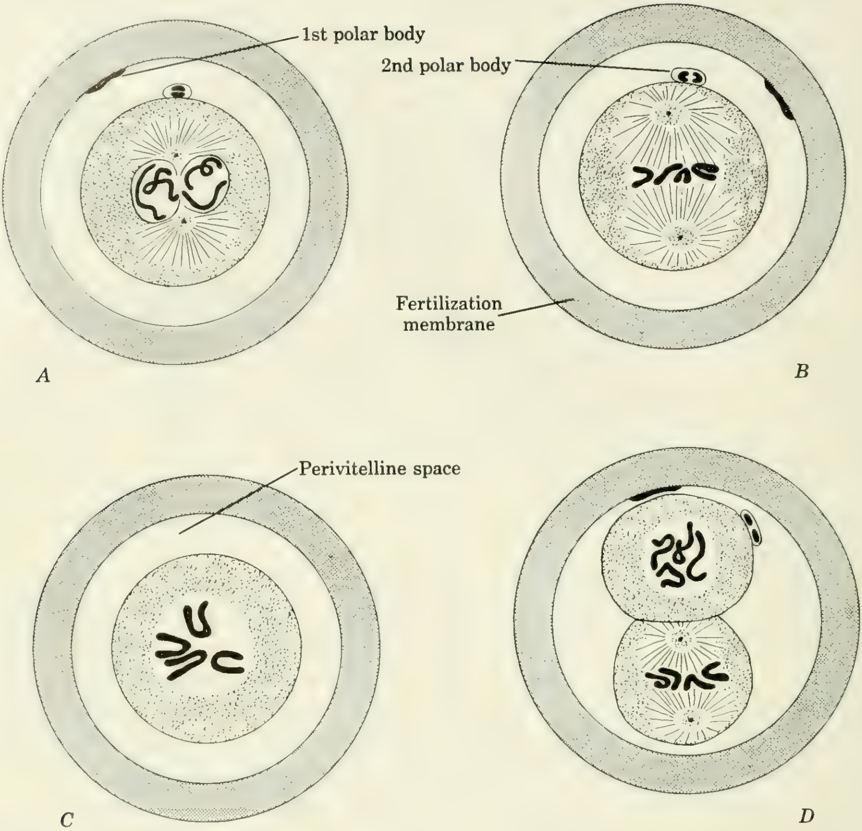


Fig. 5.11. Amphimixis and early cleavage in *Parascaris equorum* (*Ascaris megalocephala bivalens*), a nematode. *A*, the male and female pronuclei have approached one another as the mitotic spindle for the first cleavage is formed; each contains two chromosomes, the haploid number. *B*, the four chromosomes (diploid number) at the equatorial plate of the first mitotic spindle, seen from the side. *C*, the four chromosomes at the equatorial plate of the first mitotic spindle, seen from one end of the spindle. *D*, a two-cell stage in which both nuclei are in the late prophase of mitosis (the second cleavage). All figures ×640.

Fertilization. The union of an egg and spermatozoon is known as fertilization, or syngamy, and the resulting cell, which has the capacity to develop into a new individual, is called a zygote. Two separable and very important phenomena, which were recognized almost immediately, are observed during fertilization. In 1875 Hertwig appreciated the fact that it is the union of spermatozoon and egg that stimulates the egg to begin its development; this aspect of fertilization is known as **activation**. Not until 1883, when Van Beneden studied fertilization in *Parascaris*, was the additional significance of the fusion of cells from two parents recognized. Fol had observed meiosis in 1875, but Van Beneden had much more favorable material and could see that the nuclei of spermatozoon and ovum contributed equally to the nuclear constituents of the zygote (Fig. 5.11). The union of two pronuclei, each containing one chromosome of each of the homologous pairs characteristic of the species, restores the diploid number of chromosomes and is known as **amphimixis** (p. 41). Each zygote, consequently, has the same number of pairs of chromosomes that each of its parents has, and each parent contributes one chromosome of each pair. Meiosis and amphimixis furnish the physical basis for an understanding of heredity (pp. 185–194).

Meiosis and spermiogenesis occur in the seminiferous tubules of the testis, and the spermatozoa are mature when they are shed by the male and penetrate the eggs. The female germ cells are not always mature when the spermatozoa enter. The primary oöcytes, surrounded by their follicles, grow and store nutrients in the ovary, and in some animals both meiotic divisions occur before ovulation; ova are liberated and fertilized. In other animals the primary oöcyte is ovulated, and the spermatozoon enters before either meiotic division has occurred (Fig. 5.9). Meiosis begins in many vertebrates just before the time of ovulation, and the spermatozoon enters either the primary or secondary oöcyte, which then completes its meiosis. When it enters an immature egg, the spermatozoon remains quiescent until oögenesis is completed. The nucleus of the spermatozoon, or **male pronucleus,** then becomes rounded and vesicular like the **female pronucleus** before amphimixis takes place.

As long ago as 1785, when Lazaro Spallanzani mixed lemon juice and vinegar, among other things, with frogs' eggs in an attempt to stimulate them to develop, biologists sought to secure activation by artificial means. Finally, in 1899, Jacques Loeb succeeded in finding a method of **artificial parthenogenesis,** as the experimental activation of an egg that normally unites with a spermatozoon is called. A few years later Loeb was able to rear to maturity frogs that had developed from artificially activated eggs; these frogs had a mother but no father. It is now known that a variety of methods will initiate development in eggs that normally develop only after fertilization. George Lefevre, Sr., in 1907 used dilute organic acids (Fig. 5.12); others have used heat, shaking, pricking of the surface of frogs' eggs, and various chemical agents. Most of the studies on artificial parthenogenesis have been on the eggs of invertebrates, but in recent years attempts have been made, with some success, to activate mammalian eggs artificially. It has been stated that parthenogenesis occurs normally in some insects, notably bees and aphids, and among the rotifers. Parthenogenesis, whether normal or artificial, can be induced only when the egg cell is in a certain stage, which may be called a fertilizable condition, and corresponds only to the activation aspect of fertilization. There is only one parent, and amphimixis cannot occur.

Fertilization depends not only on the fertilizable condition of the egg but also on the ability of the spermatozoa to come in contact with the egg. The flagellate spermatozoon of vertebrates swims by lashing its tail; fertilization can occur only in liquids. The lower vertebrates, such as the frogs, typically copulate as the eggs are passed from the body of the female, so that the

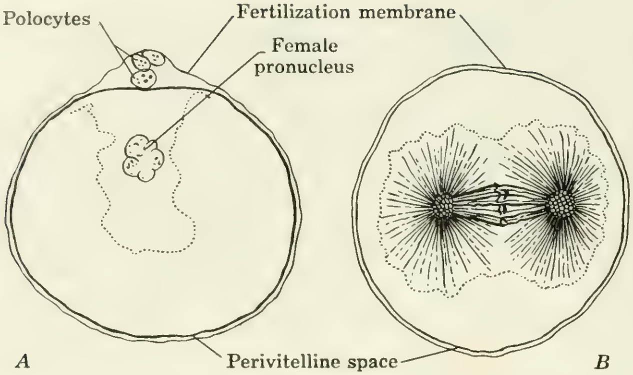


Fig. 5.12. Early development after artificial parthenogenesis in *Thalassema*, a worm-like invertebrate. *A*, meiosis has occurred within a fertilization membrane, the formation of which was conditioned by a short treatment with dilute acid. *B*, the first cleavage spindle; only the haploid number of chromosomes is present. (From G. Lefevre, 1907, *Journal of Experimental Zoölogy*, vol. 4.)

spermatozoa are shed over the egg mass in the water. Fertilization takes place in the water, outside the body. In vertebrates that live on the land, fertilization is internal. Copulation occurs, and spermatozoa are introduced into the reproductive tract of the female, where they can swim in the seminal fluid and in the liquid filling the female ducts. The spermatozoa pass into the Fallopian tubes and meet the eggs as they are ovulated. In most reptiles and birds additional food material in the form of albumen is secreted about the fertilized egg, or zygote, as it passes down the oviduct. A shell, which prevents drying and serves as a protection for the developing individual, is added before the egg is laid or passed out of the female's body to develop (Fig. 5.4). The mammalian zygote is retained and nourished in the uterine portion of the oviducts during the developmental period.

Usually only one spermatozoon penetrates an egg cell, but in some vertebrates, such as the birds, **polyspermy** is a normal occurrence; that is, several spermatozoa enter each egg. However, the nucleus of only one of these spermatozoa fuses with the egg nucleus in amphimixis. In 1875, Fol observed that, as soon as one spermatozoon had reached the egg, a membrane, known as the **fertilization membrane,** becomes separated from the surface of the egg, leaving a **perivitelline space** around the egg (Figs. 5.9 and 5.11). The fertilization membrane was believed by many students to be a device to prevent polyspermy but is now recognized as a by-product of activation. Such a membrane is formed when eggs are artificially stimulated to develop (Fig. 5.12). The spermatozoon swims actively until it comes in contact with the surface of the egg; the egg then engulfs the spermatozoon after first sending out a minute projection, the **entrance cone,** in which it becomes embedded (Fig.

5.13). The process of engulfing the spermatozoon requires only a few seconds in many animals, although it may take as long as an hour. Most often the tail of the spermatozoon is not taken into the egg; only the head containing the male pronucleus and the middle piece containing the centriole, which gives rise to the centrioles of the spindle of the zygote, are involved in fertilization (Fig. 5.8). If the tail of the spermatozoon enters the egg, it undergoes degeneration as development begins; this happens in the frog, the bat, and some other animals.

Development

Reproduction in the vertebrates is complete when maturation, activation, and amphimixis have taken place, when the differentiated egg and sperm cells have united. The zygote is potentially a new individual; it has the capacity to develop into an organism similar to its parents in all essential respects. The process of development, which always follows reproduction by syngamy in the multicellular animals, consists essentially of cell division, cell localization, and cell differentiation. Growth occurs in all developing individuals and is responsible for the increase in the amount of protoplasm, which is correlated with the increase in cell numbers by continued cell division. Development is a continuous process in which a definite series of events occurs in a definite sequence under very limited environmental conditions. Food and oxygen are furnished, waste products are removed, excessive loss of water is prevented, and a rather limited temperature range is maintained. The methods of caring for the metabolic requirements of a developing in-

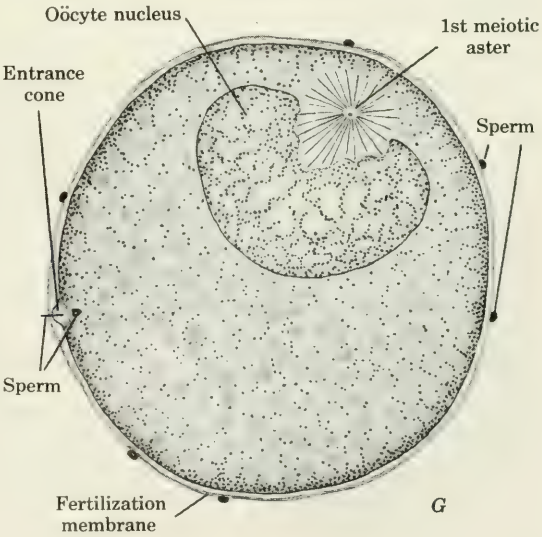


Fig. 5.13. Entrance of spermatozoön and formation of first meiotic spindle in the egg of *Thalassema* (cf. Fig. 5.12); ×820.

dividual will be discussed later (p. 159), but it may be noted here that undue evaporation is prevented during the development of terrestrial vertebrates by egg membranes and shells or by the retention of the embryo in a uterus. The range of temperature is determined in fishes, amphibians, and reptiles by the season during which the eggs are laid, and unseasonal temperatures may kill such developing eggs. Birds, of course, incubate their developing eggs; in mammals, the mother's body regulates the temperature of the embryos in the uterus. In our discussion of development we shall assume that all environmental conditions are normal. The development of a single cell into a complex, highly differentiated animal is one of nature's marvelous pageants, a series of events that occurs in such an orderly fashion as to fill the observer with awe.

The pattern of early development is correlated very closely with the amount of nutritive material stored in the oöcyte during its growth period in the ovary. In the Chordata there is a wide range in the quantity and position of the yolk in eggs. The amphioxus (p. 550), for example, has an **isolecithal egg,** so called because the relatively small amount of reserve nutrients is distributed almost uniformly throughout the cytosome. Among the vertebrates the frog has a **telolecithal egg** in which a considerable quantity of yolk is stored more abundantly in one half, the so-called **vegetal hemisphere,** than in the other half, or **animal hemisphere,** where the nucleus is always found (Fig. 5.3*B*). A more pronounced polarization of nucleus and yolk is to be seen in the telolecithal eggs of fishes, reptiles, and birds (Fig. 5.4*B* and *C*). In such eggs the nucleus is located near the animal pole surrounded by a relatively small amount of cytoplasm forming the **blastodisk,** and the large cytosome is packed with yolk enclosed by a very thin layer of cytoplasm, which lies at the surface of the egg. The egg-laying mammals produce telolecithal eggs like those of reptiles; the placental mammals have isolecithal eggs in which reserve nutrients are stored in varying amounts but never in large quantity.

As the sequence of events during the development of chordates is described, comparisons will be made between certain representative forms to call attention to the fundamental similarity of development in all, as well as to indicate special differences. Development is a continuous process, although it can be divided into stages for purposes of discussion. In the account which follows, the early stages characterized only by cell division are described under that heading. The stages during which the conspicuous mass movements of cells occur are described under the heading of cell localization; these movements separate the so-called germ layers and establish the body plan, as well as the primordia of all the organ systems. The final stages in which cytosomal differences appear in cells, with the production of tissues, are summarized under the heading of cell differentiation.

Cell Division: ***Cleavage.*** Cleavage follows activation and consists of a series of cell divisions. Cell division, of course, occurs during other periods, but during cleavage it is the only visible indication of development. What we see externally is the constriction of the cytosome during the telophase of mitosis; the orderly separation of half-chromosomes occurs before this. During the early divisions all the cells divide at so nearly the same rate that it appears as if the zygote were being cut with a knife into smaller and smaller parts. If the zygote is visualized as a globe with the north pole of the earth representing the animal pole of the zygote and the south pole representing the vegetal pole, it may be easier to understand how the zygote is divided during cleavage.

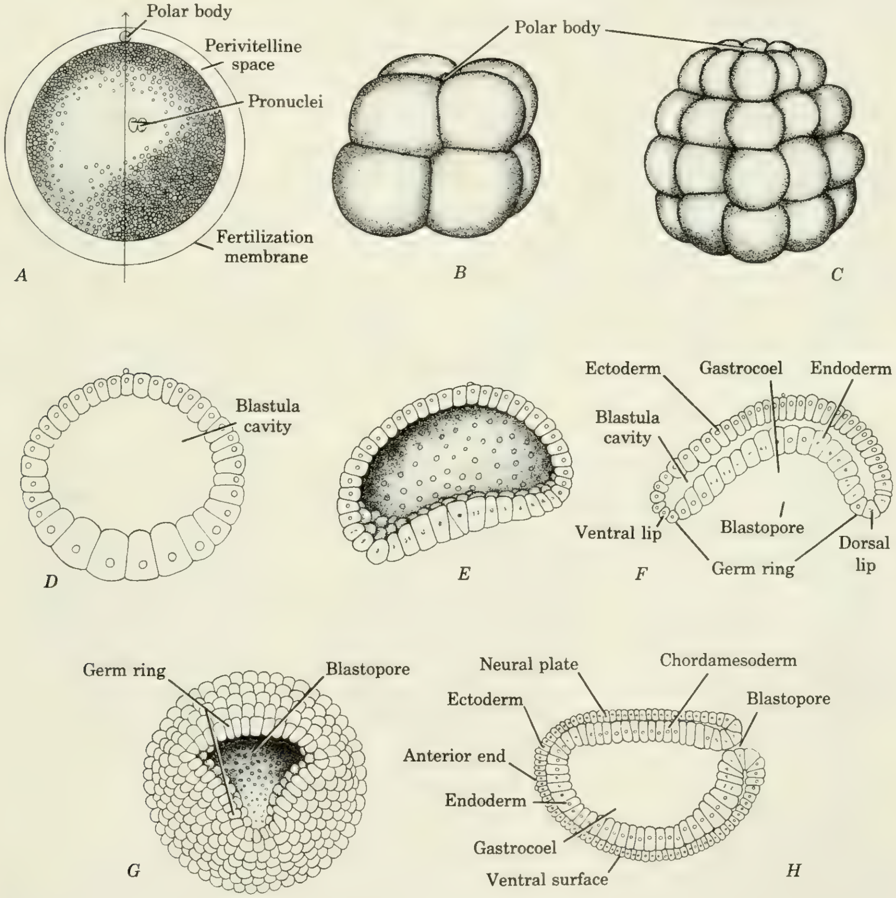

Polar body
Perivitelline space
Pronuclei
Fertilization membrane
A
Polar body
B
C
Blastula cavity
D
E
Ectoderm
Gastrocoel
Endoderm
Blastula cavity
Ventral lip
Blastopore
Dorsal lip
Germ ring
F
Germ ring
Blastopore
G
Neural plate
Chordamesoderm
Ectoderm
Blastopore
Anterior end
Endoderm
Gastrocoel
Ventral surface
H

Fig. 5.14. Early development in the amphioxus. *A*, one-cell stage, in section; the arrow indicates the egg axis. *B*, eight-cell stage, from the surface. *C*, 32-cell stage, from the surface. *D*, early blastula, in section. *E*, late blastula, as if cut in half. *F*, early gastrula, in section. *G*, gastrula, from the surface. *H*, late gastrula in section, oriented to show dorsoventral and anteroposterior axes. (*A*, *B*, and *G*, from E. G. Conklin, 1933, *Journal of Experimental Zoölogy*, vol. 64; *C–F* and *H* from E. G. Conklin, 1932, *Journal of Morphology*, vol. 54.)

In the amphioxus (*Branchiostoma lanceolatum*) cleavage is **total**; that is, the entire zygote is divided into two cells of the same size, and division continues to produce cells that differ but little in size (Fig. 5.14*B* and *C*). The cleavage pattern is like that of the frog, in which cleavage is also total but in which inequality in the sizes of cells is soon apparent. In the frog the plane of the first **cleavage furrow**, as the cytosomal constriction is called, passes from the animal to the vegetal pole. Usually one of the resulting cells is destined to give rise to the right side of the individual, the other to the left side. This fact has been established because of certain changes that occur in the frog's egg after the entrance of the sperm. The sperm enters at some point in the animal hemisphere, and as the second meiotic division occurs, streaming movements in the cytoplasm result in a distribution of material with reference to the plane of entrance of the sperm and the path it follows as it is carried toward the egg nucleus (Fig. 5.15*A* and *B*). These streaming movements of the cytoplasm, in addition to producing invisible localization of cytoplasmic regions, give rise to the **gray crescent**, an area from which some of the pigment is carried away and which lies approximately opposite the entrance point of the sperm. With this visibly different region as a landmark, observations can be made concerning the fate of certain regions of the zygote during development. Thus, it has been determined that the future median longitudinal plane of the embryo coincides with a plane passing through the egg axis and bisecting the gray crescent (Fig. 5.15*B*). Since the first cleavage plane usually bisects the gray crescent, it follows that bilateral symmetry becomes apparent at this time.

The second cleavage furrow likewise appears first at the animal pole and passes to the vegetal pole at right angles to the first, so that a four-cell stage results. These cells are of equal size, but cleavage now becomes unequal in the frog. The third cleavage furrow cuts each of the four cells in a plane parallel to the equator but nearer the animal than the vegetal pole. Of the resulting eight cells, the four in the animal hemisphere are smaller. Two fourth cleavage furrows appear simultaneously in the smaller cells and pass through the larger cells to form a 16-cell stage. After this, two fifth cleavage furrows, one on each side of the third cleavage furrow, produce 32 cells. Indications of an irregularity of division rate can often be seen during the fourth and fifth cleavages, since the furrows pass more rapidly through the cells containing less yolk.

Formation of the Blastula. As the egg divides during cleavage, the cells tend to become spherical. Since the yolk stored in the female germ cell is being utilized as the source of energy for cleavage, a small cavity appears internally as early as the eight-cell stage in the frog. This cavity is quite conspicuous after the fifth cleavage and is known as the **cleavage cavity**, **blastula cavity**, or **blastocoel**. The developing individual is now called a **blastula**, and this period in development is referred to frequently as the **blastula stage**. The blastula arises as a result of cell division only; no cell movements have occurred. If the egg is isolecithal and cleavage is total and

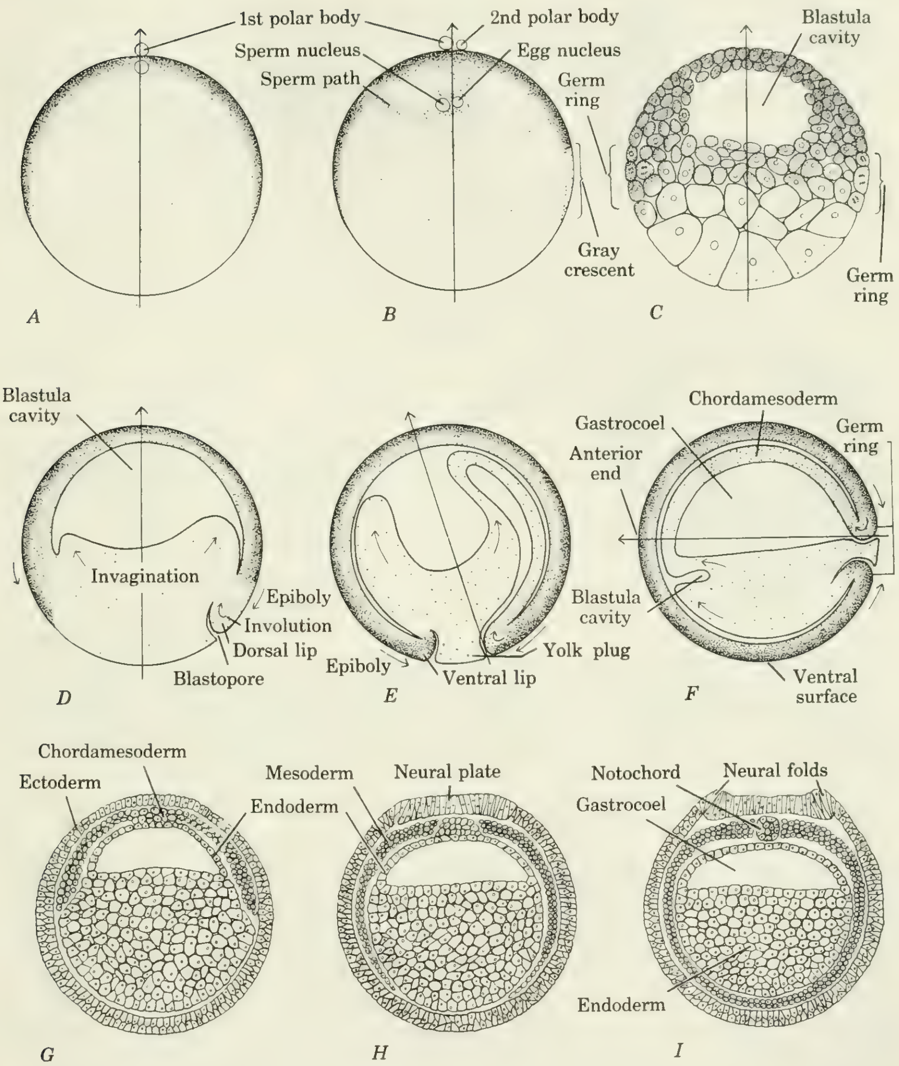

1st polar body
2nd polar body
Sperm nucleus
Egg nucleus
Sperm path
Germ ring
Gray crescent
Blastula cavity
Germ ring
A
B
C
Blastula cavity
Invagination
Epiboly
Involution
Dorsal lip
Blastopore
D
Epiboly
Ventral lip
Yolk plug
E
Chordamesoderm
Gastrocoel
Germ ring
Anterior end
Blastula cavity
Ventral surface
F
Chordamesoderm
Ectoderm
Mesoderm
Endoderm
Neural plate
Notochord
Neural folds
Gastrocoel
Endoderm
G
H
I

Fig. 5.15. Early development in the frog. *A*, egg before activation, in section. *B*, one-cell stage before amphimixis, in section. The first cleavage furrow would pass in the plane of the paper, through the egg axis, and bisect the gray crescent. *C*, late blastula, in section. *D*, early gastrula, in section. *E*, gastrula in section. *F*, late gastrula, in longitudinal section, oriented to show dorsoventral and anteroposterior axes. *G*, *H*, and *I*, embryos during the formation of the notochord, the dorsal mesoderm, and the neural plate, in cross section. All figures diagrammatic; the arrow indicates the egg axis. (*E* and *F*, redrawn with modifications from R. S. McEwen, *Vertebrate Embryology*, copyright 1931 by Henry Holt and Co., printed by permission.)

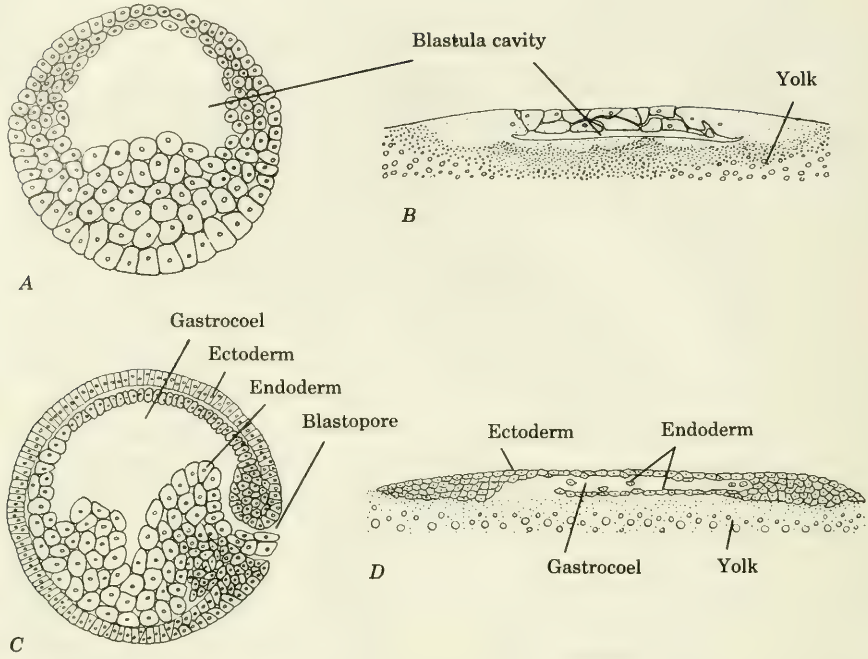


Fig. 5.16. Blastulae and gastrulae of amphibians and birds. *A*, blastula of *Triton*, a salamander. *B*, blastula of the domestic fowl. *C*, gastrula of *Triton*. *D*, gastrula of the chick (cf. Fig. 5.6*B*). (*A* and *C*, redrawn from O. Hertwig, *Lehrbuch der Entwicklungsgeschichte des Menschen und der Wirbelthiere*, 1890; *B*, redrawn from J. T. Patterson, 1910, *Journal of Morphology*, vol. 21.)

approximately equal, the blastula cavity is located centrally and surrounded by cells of similar size, as in the amphioxus (Fig. 5.14*D*). In the amphibians, where the egg is telolecithal and cleavage is total but unequal, the blastula cavity is in the animal hemisphere and has a roof of small cells and a floor of large cells (Fig. 5.16*A*). Further, in the fishes, reptiles, and birds in which the egg is telolecithal and cleavage occurs only in the blastodisk, or small amount of cytoplasm surrounding the nucleus at the animal pole, the blastula cavity lies between the disk of cells and the underlying, undivided yolk mass (Figs. 5.4*B* and *C* and 5.16*B*). The blastula cavity in forms like the amphibians and birds is filled with a solution of food material that diffuses into it from the yolk-laden cells or yolk mass of its floor.

Cell division continues during the blastula stage. In the frog the cells divide parallel to the surface of the blastula so that the blastula cavity becomes roofed by several layers of cells. An equatorial belt of cells, which is not visibly different from other parts of the animal hemisphere, is known as the **germ ring** and plays a very important role in later development (Fig. 5.15*C*). The cells formed in this region spread toward the vegetal pole.

Since these cells are pigmented, the direction and extent of their movements can be noted; the original location of the gray crescent can still be observed. The establishment of the germ ring and the beginning of its shift in position mark the end of that part of development in which cell division is the characteristic event. Cell division, however, continues, and the number of cells increases greatly during the next period of development.

In eggs that do not have a natural marker such as the gray crescent of some amphibian eggs, it has been possible to mark different parts of the blastula by means of non-toxic or vital dyes. It has been found that certain limited areas of the blastula always move, in the normal course of development, to a specific part of the gastrula. These regions whose developmental fate, so to speak, is already determined at the blastula stage are called **presumptive areas.**

Cell Localization. The spread of cells formed at the original equatorial region of the zygote toward the vegetal pole is the beginning of a phase of development characterized by mass movements of cells which lead to the establishment of the so-called body plan of the chordate. During this period of cell localization masses of cells are brought into new relations with one another. The embryo is presently found to consist of three distinguishable layers of cells which have long been called the **germ layers,** namely, ectoderm, endoderm, and mesoderm. The first part of cell localization is frequently referred to as gastrulation.

Gastrulation in the amphioxus is a much simpler process than in amphibia, where yolk-laden cells are a complicating factor in the movements that occur. In the amphioxus the late blastula becomes somewhat flattened at the vegetal end, the cells of which begin to move as a group into the blastula cavity (Fig. 5.14*E–H*). This is known as the process of **invagination.** The open end of the early **gastrula,** as the developing individual is now called, is known as the **blastopore,** and the cells of the germ ring form its **lips.** The movements of the cells continue until the blastula cavity is obliterated completely and there is a new internal cavity, the **gastrula cavity, gastrocoel,** or **archenteron,** which opens externally by way of the blastopore. As a result of the shifting of cells the individual now consists of two layers of cells, an outer layer of **ectoderm** and an inner layer containing the primordia of the other two germ layers, which will be sorted out by subsequent movements. The outer and inner layers are continuous with one another in the region of the germ ring, that is, at the lips of the blastopore. Continued cell divisions add cells to both these layers, and the gastrula becomes elongated as the germ ring decreases in circumference. This decrease in size of the germ ring is also known as the closure of the blastopore, which becomes smaller and smaller. This stage in the development of chordates is suggestive of the so-called diploblastic, or two-layered, body plan of some coelenterates (pp. 226 and 284).

Gastrulation in amphibia is essentially the same as in the amphioxus. The yolk-laden cells tend to move toward the blastula cavity, but invagination is not the conspicuous process that it is in amphioxus (Fig. 5.15*D*). A more noticeable activity is the overgrowth of the cells of the vegetal hemisphere by those of the animal hemisphere, so that the pigmented area increases; the non-pigmented area decreases in extent. As the spread of the pigmented cells occurs, the region of the gray crescent can still be identified, and at the pigmented border of this region an inward movement of cells begins. In other words, the cells derived from the gray crescent come to lie inside the gastrula in the region of the dorsal lip of the blastopore and in what is to be the mid-dorsal region of the embryo. The part of the germ ring from which inturning first occurs is known thenceforth as the **dorsal lip of the blastopore**, or the opening into the gastrocoel. Soon the inward shift of cells, or **involution**, occurs along the entire margin of the germ ring, which thus becomes the lips of the blastopore. In amphibia the blastopore is plugged with cells of the vegetal hemisphere which have not shifted their position (Fig. 5.15*E*). The overgrowth of the yolk-laden cells by pigmented cells is known as **epiboly** and continues, with the resulting decrease in the circumference of the germ ring and in the area of the yolk plug, until the yolk plug is covered and the blastopore is a minute opening. Internally, the gastrula cavity increases greatly in extent as a result of invagination and involution, while the blastula cavity decreases in size as the gastrula cavity expands. As gastrulation progresses, it is possible to distinguish dorsal and ventral surfaces, as well as anterior and posterior ends, because of their subsequent development. Furthermore, the expansion of the gastrula cavity in the dorsal half of the gastrula and the obliteration of the blastula cavity in the animal hemisphere result in a rotation of somewhat more than 90 degrees in the position of the individual within its jelly envelopes. Instead of the animal hemisphere, the dorsal half now floats uppermost.

As the blastopore closes in amphibia, the shift of cells from an external to an internal position is completed. The cells which remain on the surface are the ectoderm; those which have moved in and now line the gastrocoel dorsally and laterally are the presumptive notochord and mesoderm. Farther down along the sides of the gastrocoel the inwardly shifted cells are the true **endoderm.** In the floor of the gastrula cavity these cells receive additions from the yolk-laden cells by a process of **delamination**, or rearrangement, to form a definite layer. Laterally, at the junction between the endoderm and the presumptive mesoderm, a separation occurs between the two. Division of cells in each region extends the layers. The two sheets of endoderm move dorsally until they meet one another in the mid-dorsal line to form a continuous lining for the gastrula cavity. This changes the presumptive mesoderm into a middle layer, the true **mesoderm**, lying between the ectoderm and endoderm. Its free ventral margin on each side extends until the two sheets meet midventrally. Dorsally, the mesoderm is continuous with a median mass of cells derived by involution from the dorsal lip of the blastopore (Fig. 5.15*G*). This association constitutes the **chordamesoderm.** Presently the sheets of the mesoderm are no longer continuous with the mid-dorsal cells, which become arranged as a longitudinal cord of cells known now as the

notochord (Fig. 5.15*H* and *I*). Somewhat later the characteristic cavity of the mesoderm appears; this is the **coelom** (Fig. 5.17). With the localization of the three germ layers and the formation of the archenteron and the coelom as cavities surrounded, respectively, by the endoderm and the mesoderm, the fundamental triploblastic body plan of the chordates has been established.

The establishment of the typical body plan is only the beginning of cell localizations. Within each of the three layers movements of lesser masses of cells occur and give rise to the primordia of the organ systems of the adult vertebrate.

At the same time that the mesoderm and notochord are being localized, the first stage in the formation of the **nervous system** occurs. The ectoderm over the chordamesoderm becomes thicker and is known as the **neural plate** (Fig. 5.15*H*); when this occurs the embryo is sometimes called a **neurula**. Along

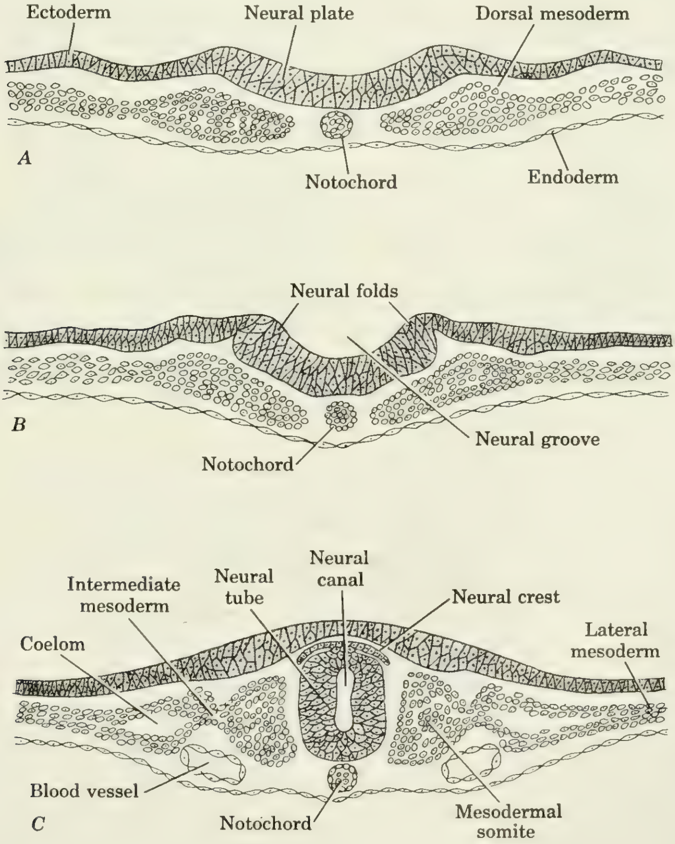

Ectoderm
Neural plate
Dorsal mesoderm
A
Notochord
Endoderm
Neural folds
B
Notochord
Neural groove
Neural canal
Intermediate mesoderm
Neural tube
Neural crest
Lateral mesoderm
Coelom
Blood vessel
C
Notochord
Mesodermal somite

Fig. 5.17. The localization of the neural tube in the domestic fowl. *A*, *B*, and *C*, successive stages, in cross section. (Redrawn with modifications from M. Duval, *Atlas d'embryologie*, 1889.)

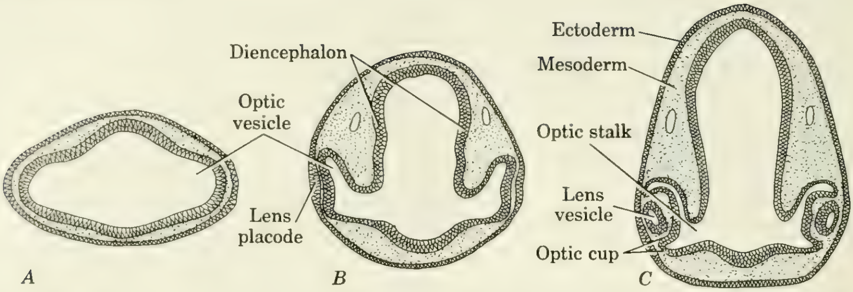


Fig. 5.18. The early development of the eye. *A*, *B*, and *C*, cross sections through the heads of chick embryos, showing successive stages in the localization of the various parts of the eye.

the lateral edges of this thicker plate of **neural ectoderm**, where it is continuous with the thinner **superficial ectoderm**, folds appear on the surface of the embryo. These are the **neural folds**, which move toward the dorsal midline, where they meet and fuse. This fusion unites not only the edges of the neural plate to form the **neural tube** but also the edges of the superficial ectoderm that covers the entire surface of the frog embryo and gives rise to the epidermis of the skin (Figs. 5.15*I* and 5.17). During the closure of the neural folds some ectodermal cells are left between the superficial ectoderm and the neural tube; they form the **neural crest.** The neural plate is wider at its anterior end than it is toward the blastopore, and the neural tube is consequently larger at the anterior end. Thus, from a very early period, the anterior region is distinguishable as the part destined to give rise to the **brain**, and the posterior part is marked as the region which is to give rise to the **spinal cord** (Fig. 5.19). Within the brain region localized expansions produce first three and then the five **brain vesicles** which are characteristic of all vertebrate embryos (Fig. 5.21).

The formation of the eye occurs at the time when the brain vesicles are established in vertebrates. Near the anterior end of the brain, expansions appear to the right and left; these are the **optic vesicles** (Fig. 5.18). Later the outer cells of these vesicles move in to produce the **optic cups.** At the same time the superficial ectoderm covering the optic cup thickens and folds in to form the **lens vesicle**, which is later cut off and forms the **lens** of the eye (see Fig. 4.3, p. 89).

The first stage in the establishment of the **digestive system** is seen when the endoderm and archenteron are formed, although the blastopore does not persist as the posterior opening of the alimentary canal. A depression of superficial ectoderm occurs posteriorly to form the **proctodeum** (Fig. 5.19*A*) and anteriorly to form the **stomodeum.** These pits, lined with ectoderm, become the most posterior part of the digestive tract and the mouth cavity, respectively (p. 48). The **liver** and **pancreas** arise as outgrowths from the archenteron and are lined with endoderm. Closely associated with localizations related to the digestive system are those of the **respiratory system.** In the pharyngeal region of the alimentary canal paired pouches extend to the surface ectoderm in which slits appear (Fig. 5.20). These **gill slits** or **clefts** make possible a flow of water through the pharynx in adult fishes and certain amphibians, including the tadpole of the frog. **Gills** are developed later in this region. Such pharyngeal pouches and at least vestigial gill slits are characteristic of all chordate embryos (Figs. 5.21 and 5.22). In terrestrial vertebrates the **lungs** and **air tubes** are also formed by an outgrowth from the endoderm lining the pharyngeal region of the primitive gut.

The mesoderm undergoes many changes in the period after its localization. Most conspicuous is the proliferation that occurs along the sides of the neural tube, forming what is called the **dorsal mesoderm,** or **epimere.** Soon these cords of mesoderm become segmented and give rise to the **mesodermal somites** (Figs. 5.17 and 5.21). Later, after continued cell division, the cells of the somites are shifted in position. Some migrate around the notochord and neural tube and later form the vertebral column. Others make up the muscle plates, from which the **striated muscles** of the trunk arise, and still others form the **dermis** of the skin. Lateral to the dorsal mesoderm on each side there is a region called the **intermediate mesoderm,** or **mesomere,** from which

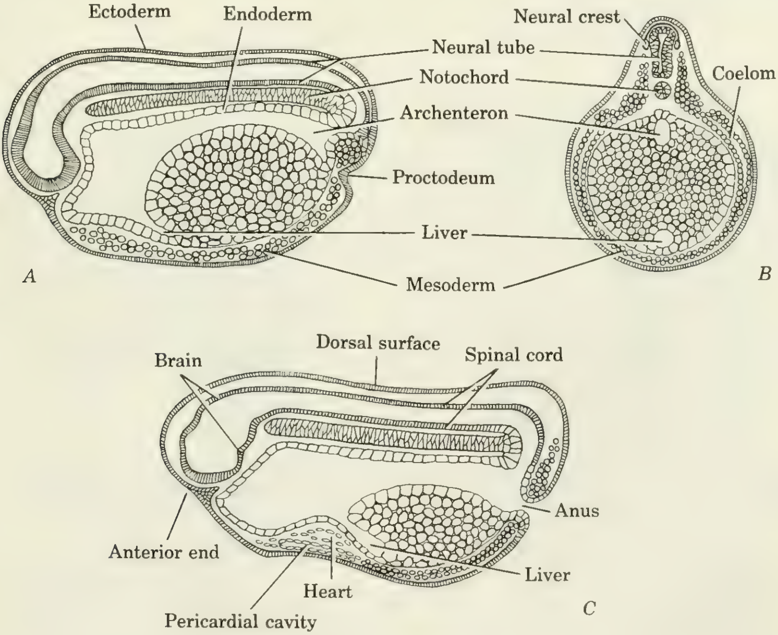


Fig. 5.19. Young tadpoles of the frog, to show localization of organ-system primordia. *A*, tadpole of about hatching age, in longitudinal section. *B*, later tadpole, in cross section; and *C*, later tadpole, in longitudinal section. All sections diagrammatic. (*A*, redrawn from T. H. Morgan, *The Development of the Frog's Egg*, copyright 1912 by The Macmillan Co., printed by permission; *C*, redrawn from J. W. Jenkinson, *Vertebrate Embryology*, copyright 1913 by Oxford University Press, printed by permission.)

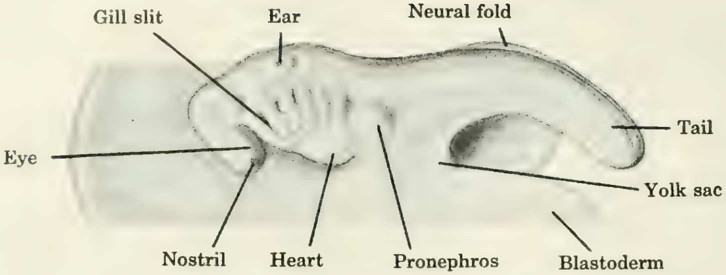

Gill slit
Ear
Neural fold
Tail
Eye
Yolk sac
Nostril
Heart
Pronephros
Blastoderm

Fig. 5.20. Embryo of the torpedo, an elasmobranch, attached to its yolk sac. (Redrawn from H. E. Ziegler, *Lehrbuch der vergleichenden Entwicklungsgeschichte*, 1902.)

the **excretory** and **reproductive systems** are differentiated (Fig. 5.17*C*). The remaining mesoderm is the **lateral mesoderm,** or **hypomere,** the cells of which become rearranged into an outer layer lying close to the ectoderm and an inner layer lying next to the endoderm (Fig. 5.17*B* and *C*). The cavity of the hypomere lying between these two layers is the **coelom** (Fig. 5.19*B*). The heart and main vessels of the **circulatory system** are established in the mesoderm (Figs. 5.19*C* and 5.21*B*).

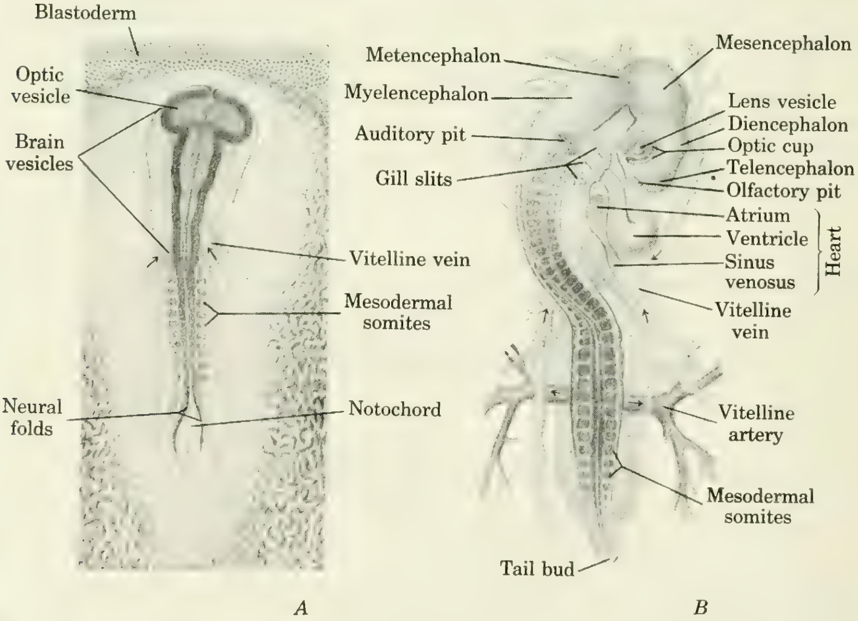
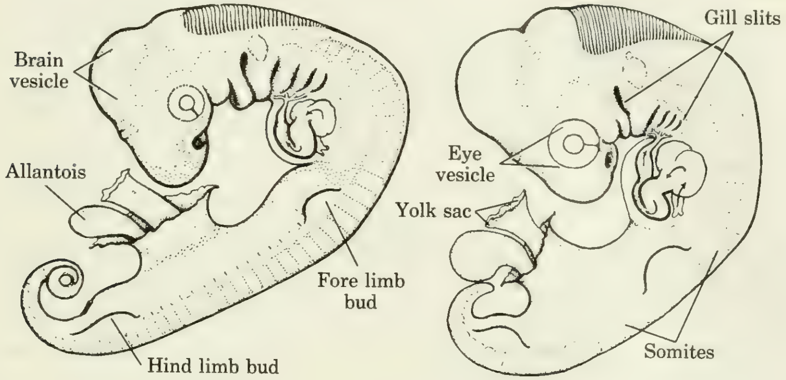

Blastoderm
Optic vesicle
Brain vesicles
Vitelline vein
Mesodermal somites
Neural folds
Notochord
Metencephalon
Myelencephalon
Auditory pit
Gill slits
Mesencephalon
Lens vesicle
Diencephalon
Optic cup
Telencephalon
Olfactory pit
Atrium
Ventricle
Sinus venosus
Heart
Vitelline vein
Vitelline artery
Mesodermal somites
Tail bud
A
B

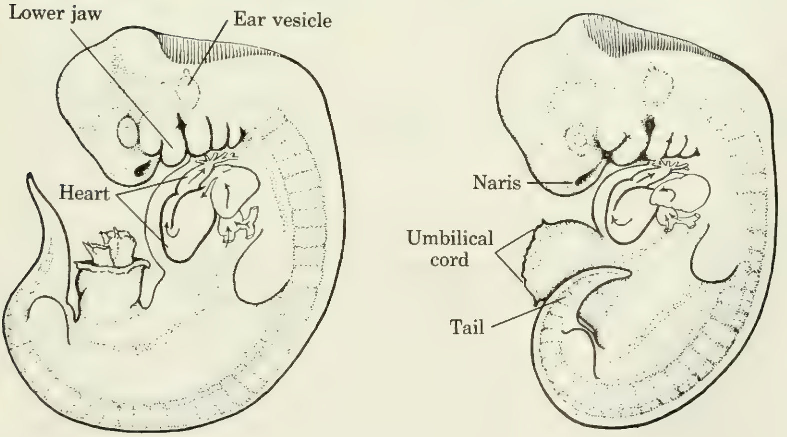
Fig. 5.21. Chick embryos, showing localization of organ-system primordia; dorsal view. *A*, embryo after 29 hours of incubation. *B*, embryo after 52 hours of incubation, with its embryonic membranes removed. Internal structures are shown as if seen through the surface. (Redrawn from M. Duval, *Atlas d'embryologie*, 1889.)

Localizations occur in different regions at the same time, but in a very orderly manner. The same degree of localization will be found in any vertebrate embryo of a given species at a given age (Fig. 5.22). Under normal environmental conditions developmental processes occur with machine-like precision.


Brain vesicle
Allantois
Fore limb bud
Hind limb bud
Gill slits
Eye vesicle
Yolk sac
Somites

Reptile

Bird


Lower jaw
Ear vesicle
Heart
Naris
Umbilical cord
Tail

Pig

Man

Fig. 5.22. Vertebrate embryos of comparable age. (Redrawn from B. M. Patten, *Early Embryology of the Chick*, copyright 1951 by Blakiston Div., McGraw-Hill Book Co., printed by permission.)

The mechanism of the cell movements that result in the shifting of the presumptive areas of the blastula to their definitive positions in the gastrula and neurula remains unknown. It is clear that the characteristic changes in

LOCALIZATION		DIFFERENTIATION
Germ Layers	Systems and Organs	Tissues
Ectoderm	Nervous system Eyes, ears, and nasal cavities Epidermis of the skin Lining of the proctodeum and stomodeum	Nervous tissue Epithelial tissue
Mesoderm	Dermis of the skin Skeletal system Wall of the digestive tract, except the lining Muscular system Circulatory system Excretory system Reproductive system Lining of the coelom	Sustentative tissue Contractile tissue Vascular tissue Epithelial tissue
Endoderm	Lining of the digestive system, except in the region of the stomodeum and proctodeum Lining of the lungs and air tubes	Epithelial tissue

Fig. 5.23. The principal localizations of cells and their differentiation during the development of the vertebrates.

shape associated with localization of specific groups of cells result from intrinsic capacities of the cells themselves. This has been shown by using enzymes to digest away the intercellular material which binds the cells of the early embryo together. Such dissociated cells will, under carefully controlled conditions, undergo the changes of shape and the movements characteristic of similar cells within the embryo.

Cell Differentiation. During the various movements of masses of cells in relation to their neighbors that occur as localization takes place, no essential changes in the character of the cells can be noted. When a group of cells has finally shifted its position, however, cell differentiation, or **histogenesis**, begins; that is, the cytosomal changes that give rise to the tissues of the adult occur. The differentiation or specialization of the somatic cells will not be described in detail. By referring to Figure 5.23 you can correlate the localizations and differentiation of development with the anatomy and histology of the adult vertebrate. Differentiation of certain kinds of somatic cells is not confined to the developmental period. Cells wear out and are replaced by others recently formed by mitosis from stocks of relatively unspecialized cells. Cells that do not become differentiated during the developmental period are known as **totipotent** or **embryonic cells** in the adult animal.

Metabolic Requirements of Embryos

The orderly series of changes which occurs during development depends on chemical reactions that take place in the cells, and these, in turn, on the metabolic requirements of the cell. A constant supply of food and oxygen must be available, and waste products of metabolism must be eliminated. The temperature, which is one factor conditioning the rate of metabolism, cannot vary widely, and drying must be prevented.

In the frog embryo, which has been used to illustrate the course of development in vertebrates, these metabolic requirements are met simply. A large amount of food is stored in the egg, the egg is laid in water from which oxygen is obtained by diffusion, and the breeding season occurs during a period of the year when temperature conditions are favorable for development. The frog embryo within the fertilization membrane is protected from adhesions, and there are no so-called embryonic membranes. As the localization of the primordia of organ systems occurs, a U-shaped **sucker** appears on the ventral surface of the head of the frog embryo, and a median posterior extension foreshadows the formation of a **tail**. The embryo hatches by slipping out of its disintegrating jelly envelopes and becomes attached to objects in the water by means of the sucker. When the stomodeum becomes continuous with the pharynx and the tail is developed further, the individual swims and feeds, although it does not resemble an adult frog. Such a self-supporting but not fully developed individual is called a **larva**; the larva of the frog is known as a **tadpole**. During the tadpole stages the frog feeds upon plants and carries on gas exchange by means of its gills, of which there is first an external and then an internal set. Toward the end of the tadpole period in development the animal begins a **metamorphosis**, or change from larval to adult structure. Hind legs and then front legs appear and grow, the tail decreases in size until it disappears, and the mouth and jaws become like those of the frog. The lungs become functional, and the gills disappear. In correlation with the change from a diet of plants to one of insects, the intestine becomes much shorter during the period of metamorphosis (p. 454). Many frogs complete their metamorphosis about 3 months after hatching, but the bullfrog usually passes its first winter as a tadpole. Such a larval period in the life cycle of a vertebrate is unusual, although larval stages characterize the development of many invertebrates (pp. 330, 375, 455, and 496).

In fishes the telolecithal eggs are laid in water, but there is one important difference in development as compared with that of the frog. Cleavage is

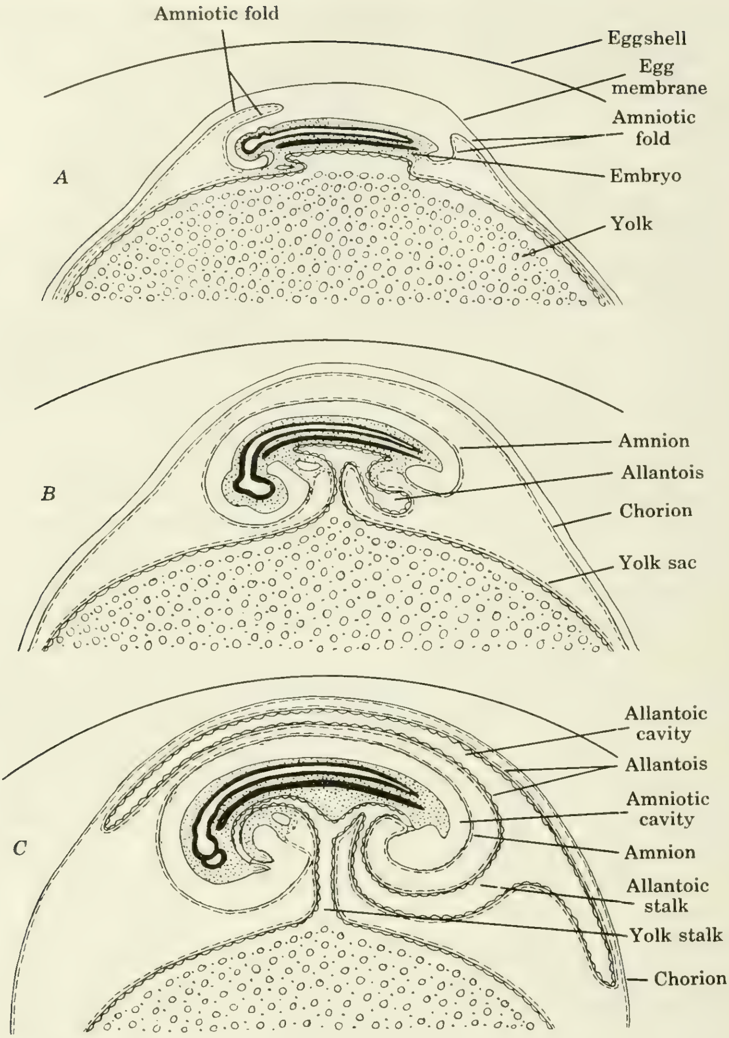

Amniotic fold
Eggshell
Egg membrane
Amniotic fold
Embryo
Yolk
A
B
Amnion
Allantois
Chorion
Yolk sac
C
Allantoic cavity
Allantois
Amniotic cavity
Amnion
Allantoic stalk
Yolk stalk
Chorion

Fig. 5.24. The embryonic membranes of the chick. *A*, *B*, and *C*, diagrams of longitudinal sections of successive stages during development. (Redrawn with modifications from T. J. Parker and W. A. Haswell, *Textbook of Zoölogy*, copyright 1921 by Macmillan and Co., Ltd., printed by permission.)

partial, and the yolk-laden part of the zygote is not divided into cells. Correlated with this fact we find the blastoderm rapidly extending over the surface of the yolk (Fig. 5.20). The cells of the endoderm and its adjacent mesoderm form a **yolk sac** which eventually encloses the yolk, and numerous blood vessels in this **embryonic membrane** absorb the yolk as it becomes diffusible and carry it to the developing embryo, which sometimes hatches before all its yolk is used.

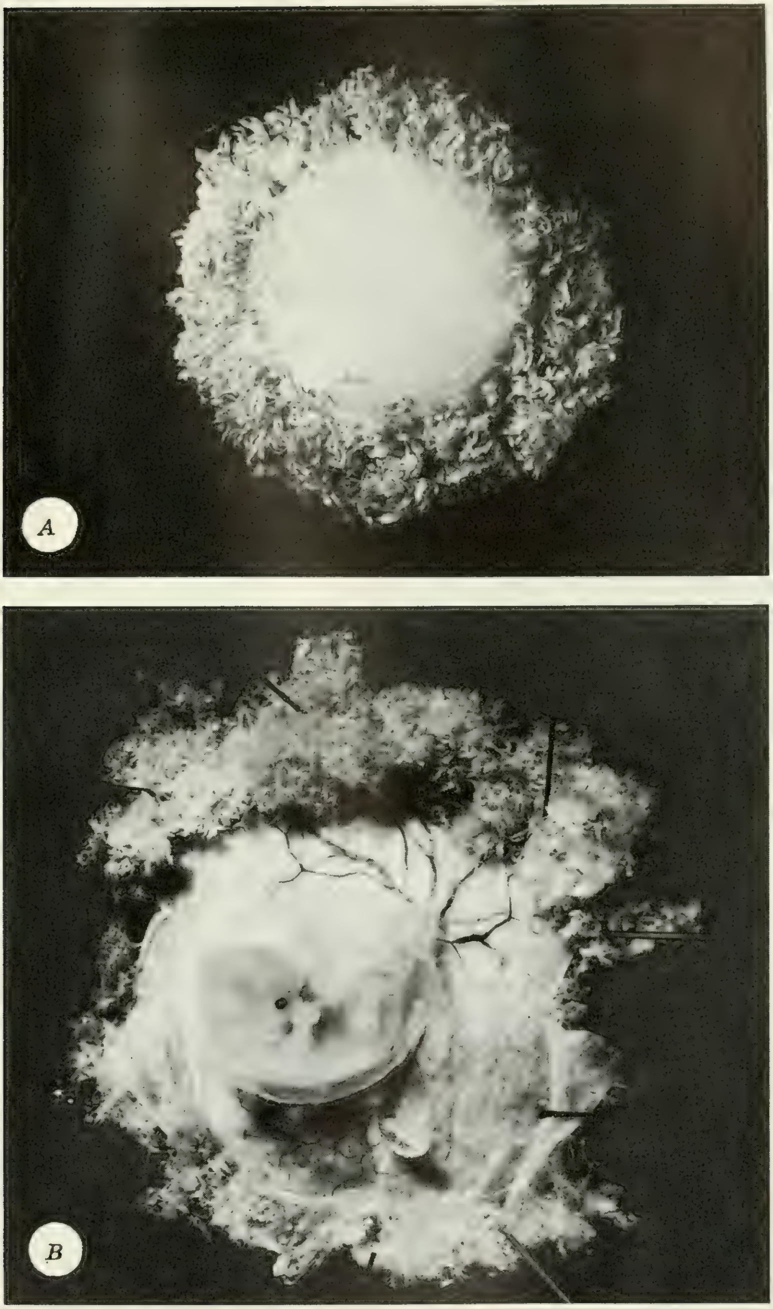


Fig. 5.25. *A*, chorionic vesicle of man removed from uterus, showing villi on surface; age, about 34 days. *B*, chorionic vesicle of man, opened to show embryo enclosed by amnion and attached to placenta at lower right; crown-rump length of embryo, 17.6 mm.; age, about 7 weeks. (Photographs courtesy Carnegie Institution of Washington, Department of Embryology.)

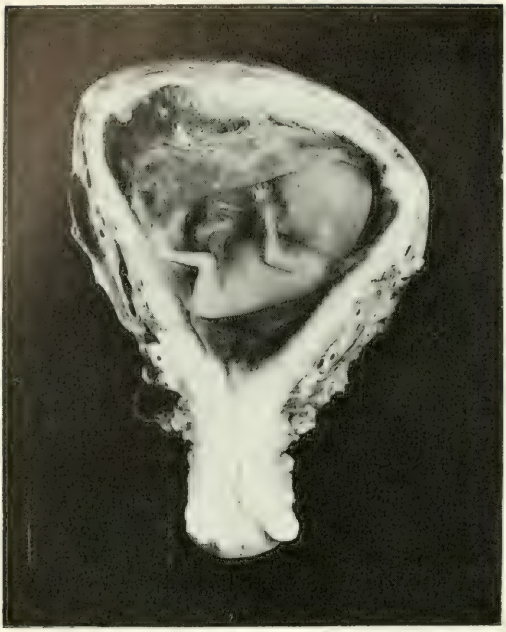


Fig. 5.26. Human fetus in uterus with chorion and amnion pulled away; the umbilical cord attaches fetus to the placenta above. The crown-rump length of the fetus is 61 mm., and its age is 10 to 11 weeks. (Photograph courtesy Carnegie Institution of Washington, Department of Embryology.)

The problem of meeting the metabolic requirements is much more complicated for the embryo of an egg-laying terrestrial vertebrate. Certain embryonic membranes always develop in such forms. They persist only during development and serve to prevent drying, furnish food and oxygen, and eliminate waste products (Fig. 5.24). A yolk sac is formed in reptiles and birds, as in fishes, and also appears as a vestigial structure in the development of mammals. In addition, the **amnion** with its enclosed amniotic fluid keeps the embryo moist and provides a protective cushion, and the **chorion** forms a protective membrane next to the shell of the egg of the reptile or bird. A fourth membrane, the **allantois,** is richly supplied with blood and lies next to the chorion. The allantois is a membrane which functions in gas exchange and excretion; it absorbs oxygen and eliminates carbon dioxide, both of which pass through the porous shells of reptiles' and birds' eggs.

Among the mammals the problem is again somewhat different. Some mammals lay yolky eggs as do the reptiles and birds; others store a certain amount of yolk in their eggs. The opossum, for instance, gives birth to very immature young which spend a considerable period in an abdominal brood pouch, nourished by milk from the mammary glands (see Fig. 18.31*C*, p. 583). In the majority of mammals, however, practically no food is stored in the egg, and development is completed within the uterus. This is made possible by the embryonic membranes, which are somewhat altered in function. During the early part of the period of cell localization the mammalian embryo becomes closely associated with the lining of the uterus. The amnion which is formed has a protective function comparable to that in reptiles and birds (Fig. 5.25*B*). The chorion, however, is the layer next to the tissues of the mother, and in man, for example, becomes concerned directly with nutrition, gas exchange, and excretion. An allantois appears during the development of the human embryo but has no function. A rich supply of blood vessels in the chorion is connected with the vessels of the embryo's body by way of vessels in the umbilical cord (Fig. 5.26). The chorion is covered with villi, or finger-like processes, that extend into blood-filled spaces in the uterine wall (Figs. 5.25*A* and 5.27). That part of the wall of the uterus in which the young human embryo becomes embedded, together with extensions of the chorion, constitutes the **placenta**. In the placenta the blood of the embryo is everywhere separated from the blood of the mother by the cells of the chorion, through which diffusion of nutrients, oxygen, and waste products occurs. There is no mechanism for regular exchange of blood between mother and embryo, although a certain amount of seepage probably occurs. In this connection it should be stated that the somewhat widespread ideas of prenatal impressions are entirely without foundation. The attachment between mother and embryo is such that diffusible substances carried by the blood can pass from one to the other. There is, however, no mechanism for the transfer of emotional conditions, unless an effect on nutrition might be so produced, and no nervous connections exist whereby reactions of the mother to unpleasant sights can affect the embryo. Only metabolic conditions can be reflected by the development of the embryo. In very few

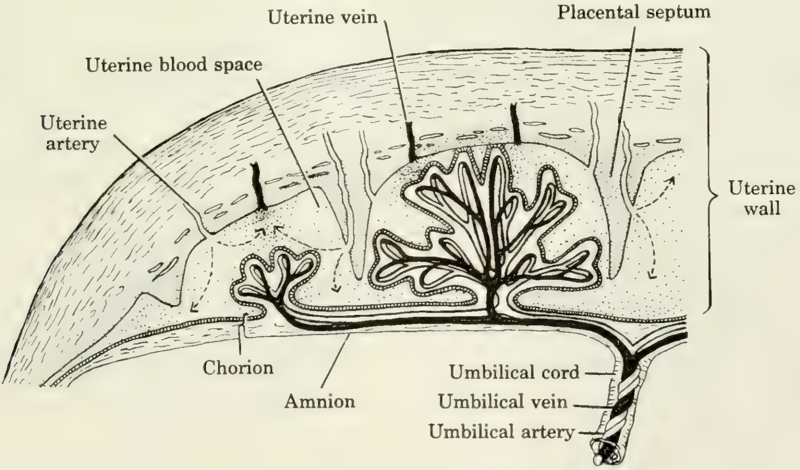


Fig. 5.27. A portion of the human placenta, in section, showing the relation between the capillaries of the embryo, which are continuous with the umbilical arteries and veins, and the blood spaces of the mother, which are continuous with the uterine arteries and veins; diagrammatic. (Redrawn from L. B. Arey, *Developmental Anatomy*, copyright 1930 by W. B. Saunders Co., printed by permission.)

instances is there any evidence of transfer of disease or poisons from the mother to the embryo in the uterus. The microorganism causing syphilis can pass the placenta and produce the disease in the fetus, as the human embryo is called after the third month. If a woman has German measles during the first 3 months of pregnancy, the causative agent passes the placenta and brings about severe effects in the embryo.

A striking illustration of another of the few disadvantages inherent in the intimate association of the embryo with its mother has been discovered. This is the origin of a very serious disease (fetal erythroblastosis) which reduces the number of red blood cells in the fetus during late pregnancy. It has been found that human red cells may have an antigen called the Rh (D) substance in addition to A and B (p. 65). Whether or not these antigens are present depends on the heredity of the individual (p. 199). Individuals who lack the Rh antigen do not normally contain an antibody for it; only 15 per cent of the general population lack the Rh antigen. If a man has the Rh substance and his wife lacks it, at least half and perhaps all their children will produce red cells containing the Rh substance. It appears certain that enough Rh-containing red blood cells, or fragments of them, pass from the blood vessels of the fetus to the blood of the mother in the placenta to stimulate the production of Rh antibodies by the mother. She immunizes herself against this foreign protein, the Rh substance. These antibodies, when they have become abundant enough, begin to diffuse back through the placenta into the blood of the fetus. Here they result in the destruction of the fetal red blood cells and, consequently, in excessive drain on the regions forming red cells, usually with fatal results. The anti-Rh substances persist in the blood of such a woman and, if her husband is homozygous (p. 186) for Rh, make it almost impossible for her to bear a second living child. Erythroblastosis results in the death of the fetus or newborn infant in slightly more than 2 per cent of the pregnancies in the white population of this country. If a partially jaundiced child born of Rh-incompatible parents is given an exchange blood transfusion within 24 hours after birth, it may be able to recover from the effects of the excessive destruction, *in utero*, of its red blood cells. In an exchange transfusion, matched Rh-negative donor blood is passed, over a period of 2 to 3 hours, into the infant's circulatory system through an umbilical vessel as the infant's blood is withdrawn. Such a procedure provides the red blood cells necessary for oxygen transport until the infant's own supply of red cells is built up in its blood-forming organs which have not been permanently damaged by the severe drain on them.

The embryonic membranes are not permanent structures. When the reptile or bird hatches, the embryonic membranes are left in the shell. After the birth of a mammal its embryonic membranes are expelled from the uterus of the mother. The development of such structures by reptiles, birds, and mammals has made them independent of an aquatic environment during development. Amphibians that are terrestrial as adults must undergo their development in the water since they have no amnion and chorion. Embryonic membranes and their modifications must have been extremely important in the evolution of the vertebrates, especially in the origin of the mammals.

Experimental Modification of Development

That the orderly processes which occur during development are conditioned by a number of closely interrelated factors can be experimentally demonstrated. The genes, or hereditary units, carried by a zygote control its development, and certain combinations of genes have been demonstrated repeatedly to bring about death in animals used in experiments (p. 205). Nuclei of embryonic cells are quite similar in appearance, and when they divide all are found to contain the number of homologous chromosomes characteristic of particular species. It has long been assumed that the nuclei of somatic cells of an individual are genetically equivalent. In recent studies, nuclei from cells of blastulae and early gastrulae as well as from cells of the chordamesoderm and endoderm of late gastrulae were transplanted singly into enucleated zygotes of the frog. Depending on the age and source of the transplanted nucleus, development of the zygote varied greatly or not at all from its normal pattern. It seems, therefore, that nuclei become differentiated in some way during development and that their differences, whatever they may turn out to be, are correlated with cell localization and differentiation.

The cytoplasm of the zygote is shifted in an orderly way by streaming movements after fertilization so that certain parts are located in particular cells during cleavage and carried into typical positions by later movements. If the zygote is subjected to strong centrifugal force so that the cytoplasm

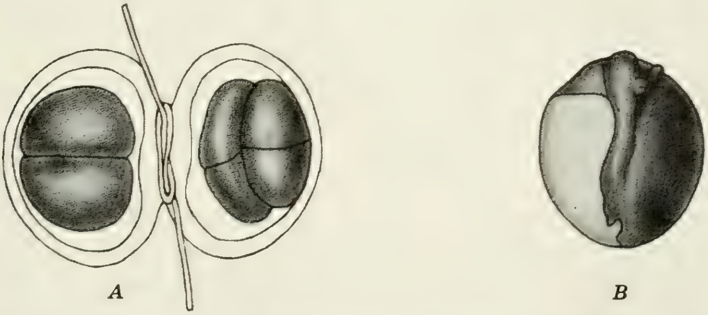


Fig. 5.28. Development of the frog after separation of cells and injury at the two-cell stage. *A*, cleavage in each part after separation of the first two cells within the jelly envelopes by constriction with a hair; each separated part gives rise to a complete embryo. *B*, a half embryo at the neural-fold stage, following injury to one of the first two cells by means of a hot needle. (*A*, after H. Spemann, 1914, *Verhandlung der deutschen zoölogischen Gesellschaft*, vol. 24; *B*, redrawn from W. Roux, 1888, *Archiv für pathologische Anatomie*, vol. 114.)

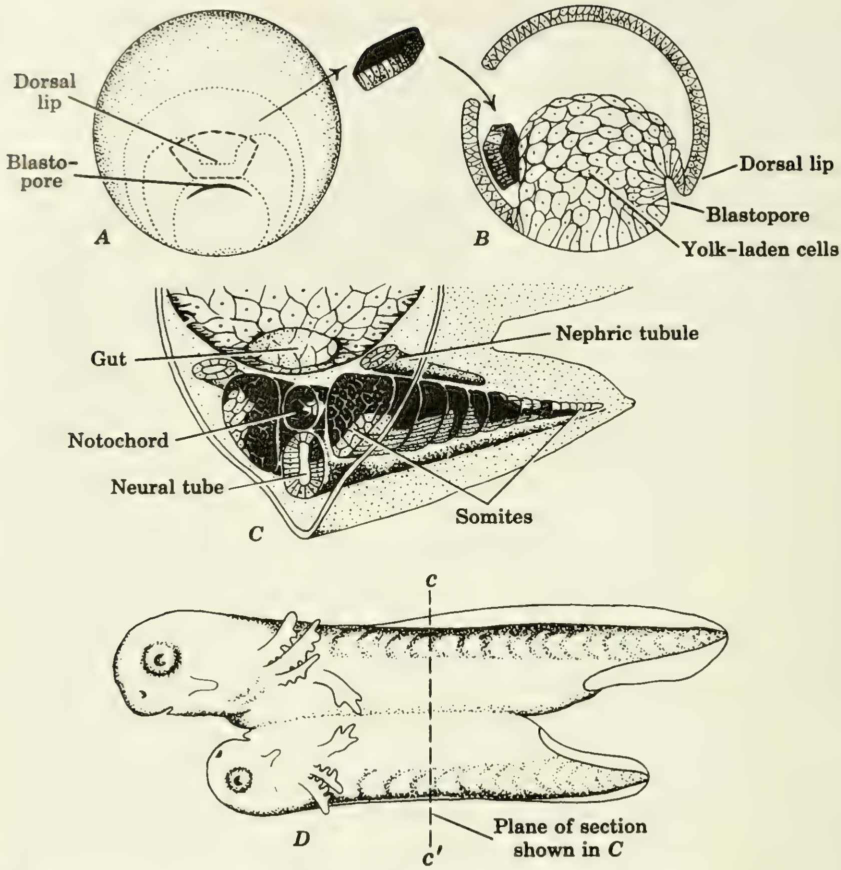

Dorsal lip
Blastopore
A
B
Dorsal lip
Blastopore
Yolk-laden cells
Gut
Nephric tubule
Notochord
Neural tube
Somites
C
c
D
c′
Plane of section shown in C

Fig. 5.29. Diagram showing results of the transplantation of a piece of dorsal lip of the blastopore of an amphibian (shown in *A*) to the blastocoel of another embryo of the same age (shown in section in *B*). In *D*, the lower individual has developed under the influence of the grafted dorsal lip; the line *c–c′* indicates the plane of the cut surface shown in *C*. In *C*, cells derived from the graft are shown in black; induced cells are in white. (Redrawn from *Analysis of Development*, edited by B. H. Willier, P. A. Weiss, and V. Hamburger, copyright 1955 by W. B. Saunders Co., printed by permission.)

is thrown out of its usual position, the course of development is not normal. This localization of cytoplasmic areas occurs more slowly in some animals than in others. If the first two cells of the frog embryo are separated, each gives rise to a whole embryo; but if one of the cells is injured, the other forms half an embryo (Fig. 5.28). In some other animals each of the first two cells will form only half an embryo if separated.

As development progresses, certain cell masses are localized and differentiate into specific organs. That this differentiation is determined in part by the relationship of the cell mass to its neighboring cells can be demonstrated by changing the typical relationships of the cells. The ectoderm on the ventral and lateral surfaces of the frog embryo normally develops into epidermis, whereas ectoderm of the mid-dorsal region gives rise to the neural plate. When the dorsal lip of the blastopore is transplanted beneath the ectoderm on the ventral or lateral regions of a frog at the gastrula stage, the ectoderm covering such a transplanted dorsal lip gives rise to a neural plate, not to epidermis (Fig. 5.29). In other words, formation of a neural plate in the mid-dorsal region is dependent on the localization of ectoderm cells in a certain relation to those cells of the dorsal lip that move internally during gastrulation. This is an example of the phenomenon of **induction.**

After localization is completely established in a region, differentiation is apparently independent of the influence of neighboring masses. The optic cup, for example, can be completely removed from an embryo and transferred to a test tube containing a nutrient solution which is changed at intervals. Under such conditions differentiation of the retina will take place, although the shape of the eyeball will not be normal, since the shape of an organ depends on the mutual pressure of adjacent cell masses. Similar indications of independent differentiation can be obtained by grafting parts of one embryo onto other embryos in a way that provides the metabolic necessities. A spectacular demonstration of the completely intrinsic nature of differentiation has been made by separating, by the use of enzymes, the cells of certain localized presumptive areas, such as the wing bud or mesonephros of the chick embryo. When masses of such dissociated cells are cultured on a nutrient clot in a moist chamber (cf. Fig. 2.5, p. 17), the characteristic tubules of the mesonephros and cartilage of the wing bud appear in due course (Fig. 5.30).

In addition to the relations between nucleus and cytoplasm and between masses of cells within the embryo, the conditions of the environment affect the course of development. Development normally occurs at a certain pace; anything that alters that rate produces an atypical embryo. This fact has been demonstrated in different ways. If the temperature is altered, the rate of development will be changed. When this is done at a time when some conspicuous mass movement of cells is occurring, as during the early stages of cell localization, later development may be atypical in many respects. If the rate of metabolism is altered by decreasing the amount of food or oxygen, similar results are obtained. One such atypical effect is the production of two embryos by one zygote. Frequently such embryos are joined, but some are entirely separate; these are identical twins, which are not produced by separation of cells during early cleavage but by some arrest of development at a later stage, probably during early cell localization. Another method of altering the metabolic rate is by the introduction of poisonous or unusual constituents into the environment. When certain salts are added to water in which frog embryos are developing, atypical localization of the optic vesicles gives rise to one median eye (Fig. 5.31).

It becomes obvious from these and numerous other experiments that development proceeds normally when a closely interlocking set of circumstances

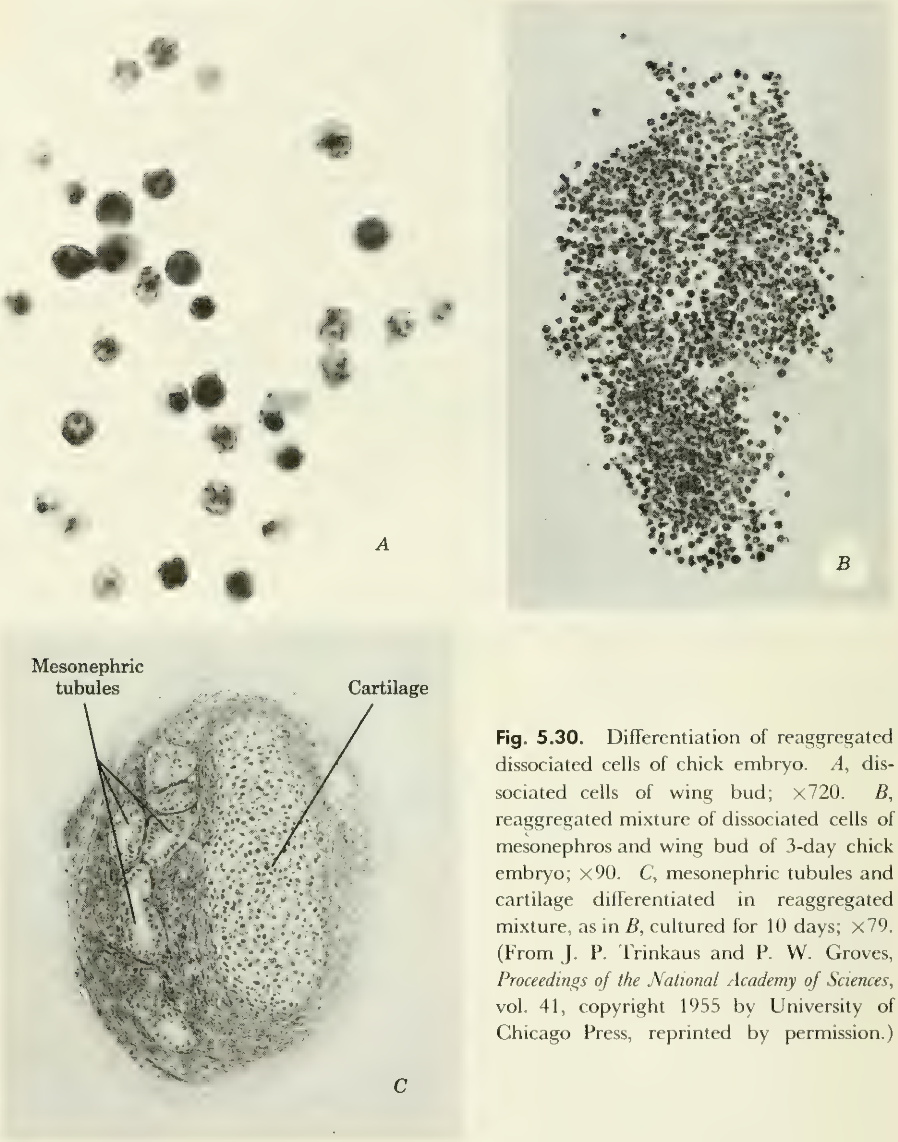


Fig. 5.30. Differentiation of reaggregated dissociated cells of chick embryo. *A*, dissociated cells of wing bud; ×720. *B*, reaggregated mixture of dissociated cells of mesonephros and wing bud of 3-day chick embryo; ×90. *C*, mesonephric tubules and cartilage differentiated in reaggregated mixture, as in *B*, cultured for 10 days; ×79. (From J. P. Trinkaus and P. W. Groves, *Proceedings of the National Academy of Sciences*, vol. 41, copyright 1955 by University of Chicago Press, reprinted by permission.)

is normal. If any condition in this group is abnormal, the orderly sequence of developmental processes will be disturbed. Relations between nucleus and cytoplasm, cell mass and cell mass, embryo and external environment can be varied but slightly if a normal individual is to develop. In the developing animal, as in the adult, the cells carry on metabolism if certain conditions are normal. The cells are also responsive and react not only to changes in neighboring cells but also to environmental changes external to the embryo.

The embryo is a living individual, potentially self-sufficient at every stage in development, yet dependent, as is the adult, upon external conditions for survival. Many problems of development remain to be solved, and many new methods of research have been devised in the attack upon the unknown in this field of zoology. It is a fascinating and a rich field for further study.

Summary

This completes your study, in the vertebrate animal, of the manifestations of life deriving from the distinguishing capacities of the cell, namely metabolism, responsiveness, and reproduction. You have seen how the different kinds of mutually dependent, specialized somatic cells perform a myriad of adaptive functions concerned with the maintenance of the life of the multicellular individual. Even in the embryo, as it develops from a single cell, this closely adjusted relationship between different cells and between cells and environment is maintained. Elucidation of the complexity of structure and function has gone forward for many years with the help of the Cell Theory, although at the present time, great contributions are being made by studies at the subcellular level.

In spite of the close attention to detail which is required to grasp the many facts presented, it is hoped that you have been stimulated to think beyond the details, even beyond the major aspects of how the problems of living have been solved at the cellular level. What really makes these intricate mechanisms go in such orderly ways? And how does it happen that the basic func-

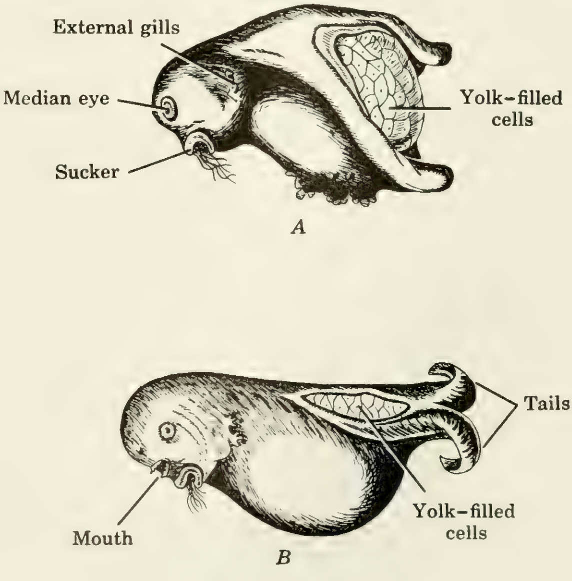


Fig. 5.31. Embryos of *Rana pipiens* treated briefly with alkali during the early gastrula stage; both are the same age. *A* has only one eye in the median position; *B* is partially doubled in the region of the spinal cord and tail. (Redrawn from *Analysis of Development*, edited by B. H. Willier, P. A. Weiss, and V. Hamburger, copyright 1955 by W. B. Saunders Co., printed by permission.)

tions such as digestion, respiration, circulation, excretion, and coordination, to say nothing of reproduction and development, are alike in all the animals of a certain kind? What determines the pattern; what perpetuates it? The importance of enzymes as directives in the chemical reactions of living cells has been pointed out in many discussions. Were we to delve more exhaustively into the "how" of life, almost innumerable instances could be cited of the ubiquity of these uniquely sculptured protein molecules which somehow provide the special niches in which the vital reactions occur. We can go a little farther in our search for a "constancy factor," a "directing agent," a "set of instructions" which is not only effective among individuals of the same generation but is handed on to successive generations. This leads to a consideration of the phenomena of heredity and variation which we shall next undertake.

CHAPTER 6

CHAPTER 6

HEREDITY AND VARIATION

What any individual is, what it can become, and what its descendants can be like is determined by its hereditary constitution, its genetic make-up. It is often said that like reproduces like, and this statement is true in a general sense. Frogs give rise to frogs, not to toads; and dogs reproduce dogs. However, the pups of a litter are not identical with their parents or with one another. A new individual resembles its parents, yet differs from them. The phenomena of heredity and variation go hand in hand. **Heredity** may be defined as the tendency of individuals to resemble their ancestors and relatives; **variation** is the tendency of organisms related by descent to differ in specific ways. New individuals arise during the process of reproduction and develop through an orderly series of changes until they reach maturity. It is obvious that whatever it is that passes from one generation to the next must determine not only the typical sequence of developmental processes but also the characteristics of the adult organism. In other words, the germ cells must carry the mechanism responsible for heredity and variation. The individual ordinarily develops under environmental conditions which are practically uniform for successive generations but which cannot be ignored in seeking the complete answer to questions concerning heredity and variation. **Genetics,** a great subdivision of zoological science which has developed conspicuously since 1900, has for its province the subject matter relating to the facts and theories of heredity and variation.

Heredity and variation can be studied by four different methods, all of which have yielded information concerning basic problems. It is possible to observe and analyze resemblances and variations from one generation to another in large groups of individuals as they are found under natural conditions. This is the **statistical method,** or the method of **biometry.** Contrasted with such mass analysis is the observation of inheritance and variation in animals bred under experimental conditions for generation after generation.

Fig. 6.1. Gregor Mendel. (A portrait by Flatter from *Journal of Heredity*, 1940, vol. 31, reprinted by permission.)

This method of **experimental breeding** under controlled conditions that give the best environment for the organisms makes it possible to know in detail the character of heredity and variation in any particular individual, as well as to compare specifically individuals of successive generations. In order to interpret fully the result of experimental breeding it becomes necessary to study, by the method of **cytology,** the germ cells from which new individuals arise. The greatest progress in the theory of genetics has come from correlation of the results obtained from experimental breeding and such study of germ cells. A fourth way of approaching the problem of the mechanism of heredity and variation is the method of **experimental embryology,** in which individuals of known ancestry are subjected to conditions that are not usual for their development. Comparison of results obtained from these several methods of approach has yielded considerable information concerning many facts of heredity and variation and has led to the formulation of theories of the mechanism involved. Clarification and extension of our knowledge of genetics may be expected to continue in view of the great amount of interest in research in this field.

The Method of Biometry

Investigators who use the biometrical method collect a great amount of observational data upon organisms under natural conditions, analyze these data by statistical methods, and formulate generalizations concerning heredity and variation that will be true for the whole group but for no particular individual. Sir Francis Galton (1822–1911) did the first serious biometrical work when he studied the relation between the height of parents and the height of offspring in over a thousand human families. The original study of

Galton on human height has been supplemented by investigations of inheritance of eye color, mental ability, length of life, and other characteristics by Karl Pearson, Raymond Pearl, and other biometricians. Under circumstances where experimental analysis and study of individual pedigrees are impossible, as is the case for most human characteristics, the biometrical method can determine trends and reveal suggestive correlations. The results of such studies do not make possible predictions concerning the inheritance of traits by the progeny of specific crosses.

Galton's observations, although made on groups that were not subjected to experimental control, furnished the stimulus for the experimental work of Wilhelm Johannsen, a Danish botanist (1857 1927). Johannsen conceived the idea that if offspring of parents who were above or below the average were also above or below the average, respectively, as Galton had found, it might be possible to shift the average by continued selection of parents from the unusual groups. Working with beans in which self-fertilization occurs, he chose the heaviest seeds from which to raise a new generation. The seeds selected weighed 0.8 gram each, and from them Johannsen obtained plants that produced seeds varying in weight from an average of 0.35 gram on some plants to an average of 0.6 gram on others. He next tried similar experiments with the seeds from single plants. The selection of the smallest seed or the largest seed for planting had no effect on the size range of the seeds produced. It was not possible to grow larger and larger beans by planting the largest seeds time after time. Since cross-fertilization did not occur, the fundamental hereditary constitution was not altered throughout the experiment. Beans descended by self-fertilization from any single plant constitute what is known as a **pure line.** Within pure lines Johannsen found that, although environmental factors of temperature, moisture, or soil might affect the size range, the average weight could not be shifted by selecting either the lightest or the heaviest beans for planting.

Johannsen was also able to demonstrate that in large groups of bean plants many pure lines are represented. Such large groups of individuals are known as **populations.** Just as each pure line varies around its average, the population varies around the average of its component pure lines. Starting with a population, it is possible to sort out, by selection of parents, lines having desired characteristics. The practical breeder tends to do this in his selections of breeding stock and seeds. However, pure lines are stable only if cross-breeding is prevented, which is frequently impossible. Selection within pure lines has been tested by many investigators. Experiments have been conducted on inheritance of size variation in different organisms, chemical content of potatoes and sugar beets, egg-laying capacity in poultry, time of maturity of seeds, distribution of color in coats of mammals, and numerous other characteristics. In no case has selection shifted the average about which a pure line varies. Such variations, which are known as **fluctuations,** are conditioned by environmental effects during development and do not influence the characteristics of succeeding generations.

The Method of Experimental Breeding

Mendel's Contribution. Although the statistical or biometrical method gives a survey of the average course of heredity and variation in populations and pure lines consisting of numerous individuals, it is not of value in the analysis of individual cases. Experimental breeding in a controlled environment makes possible the accumulation of data on the process of heredity in all the individuals produced from generation to generation. The first recorded experiment in plant breeding was that of Camerarius in 1694. Not until Father Gregor Mendel (1822 1884) of the Augustinian Order carried out his careful work on the breeding of peas in the monastery garden at Brno (Brünn), Moravia, did this method yield results that revealed the principles of heredity (Fig. 6.1). Mendel's success came when he followed the inheritance of single specific characteristics in many individuals for several generations. One of his original experiments was cross-fertilization between peas with tall stems and those with dwarf stems. The use of parents that differ in one or more characteristics is known as the method of **hybridization**, and the offspring of such a cross-fertilization are **hybrids**. If the parents differ in one characteristic, such as length of stem in peas, a cross between them is called **monohybridization**. Mendel found that without exception the offspring produced by hybridizing purebred tall and dwarf peas were tall, no matter which parent was tall and which dwarf (Fig. 6.2). When these hybrid tall peas were crossed among themselves, three-fourths of the next generation were tall like the tall parents, and one-fourth were dwarf like their dwarf grandparents. Dwarf stem, a characteristic which did not appear in the first filial generation (F_1 generation) that arose from the cross between tall and dwarf parents (P_1 generation), emerged unchanged in the second filial generation (F_2 generation). Dwarfness in such peas was as pure as was the dwarfness of their grandparents, and these F_2 dwarf peas gave rise only to dwarf peas when they were bred together. Breeding of the tall peas that constituted three-fourths of the F_2 generation revealed that, although these tall individuals superficially resembled one another, they were dissimilar as parents. One-third of the tall group gave rise in successive generations to tall offspring without exception. Such tall specimens, which constituted one-fourth of the total F_2 generation, corresponded, in their resemblance to the purebred tall pea of the P_1 generation, to that quarter of the group that was like the dwarf pea of the P_1. The remaining two-thirds of the tall peas of the F_2 generation, or one-half of the offspring of the hybrid tall peas, were like their parents. When interbred, these F_2 tall peas gave rise to offspring in the ratio of three tall to one dwarf. As shown in Figure 6.2, this group again breaks up, when analyzed by breeding, into three types that occur in the ratio of 1 : 2 : 1; that is, one-fourth are pure tall peas, one-half hybrid tall peas, and one-fourth pure dwarf peas. In the case under discussion, tallness is said to be **dominant** to dwarfness; conversely, dwarfness is **recessive** to tallness.

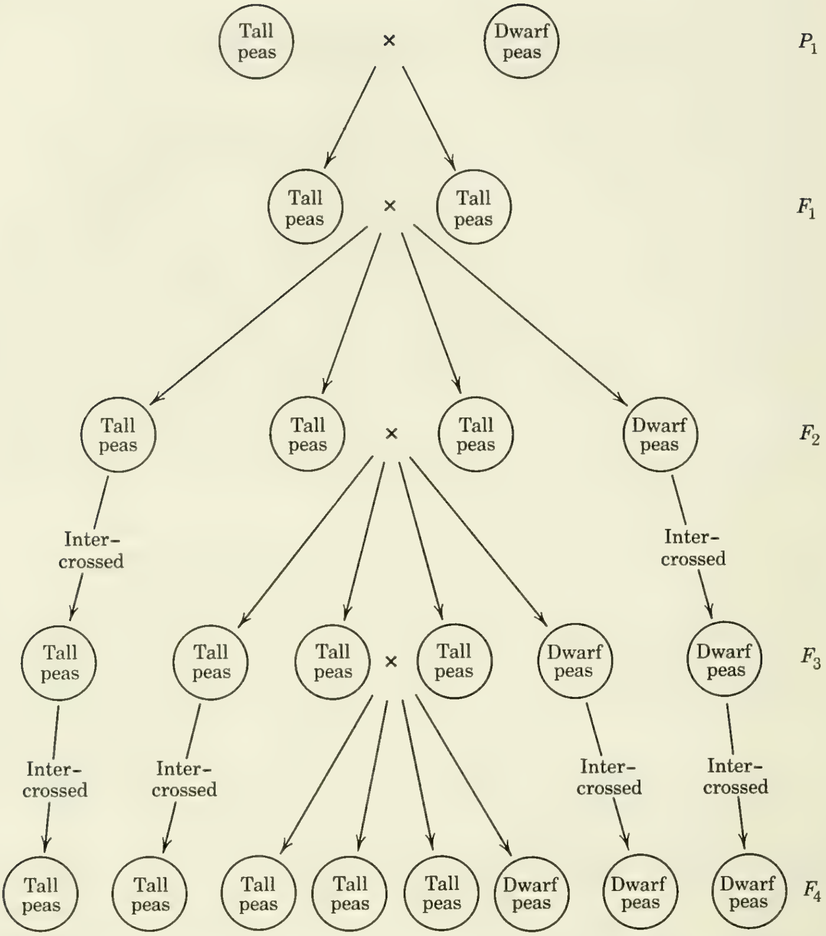

Tall peas
×
Dwarf peas
P_1
Tall peas
×
Tall peas
F_1
Tall peas
Tall peas
×
Tall peas
Dwarf peas
F_2
Inter-crossed
Inter-crossed
Tall peas
Tall peas
Tall peas
×
Tall peas
Dwarf peas
Dwarf peas
F_3
Inter-crossed
Inter-crossed
Inter-crossed
Inter-crossed
Tall peas
Tall peas
Tall peas
Tall peas
Tall peas
Dwarf peas
Dwarf peas
Dwarf peas
F_4

Fig. 6.2. Diagram to illustrate monohybridization in peas that differ in length of the stem; tall stem is dominant to dwarf stem.

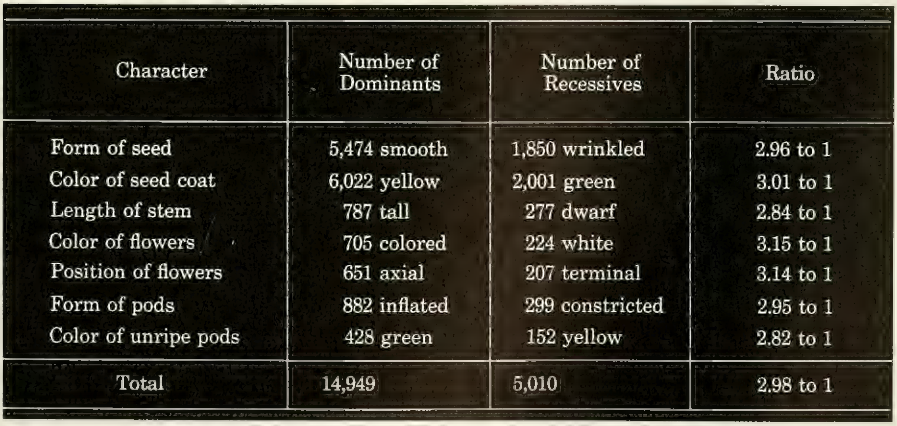
It has been stated that the offspring of a cross between tall and dwarf peas are tall. Superficially, they cannot be distinguished from the tall parent. Yet these tall hybrids when bred together give some tall and some dwarf offspring. The tall peas of the F_2 generation are all similar in appearance; but experimental breeding proves that some reproduce only tall peas, whereas others are like their parents in giving rise to both tall and dwarf offspring. In such cases of **inheritance with dominance,** it is impossible to distinguish by superficial examination a hybrid individual from an individual that will breed true for the dominant character. Johannsen proposed the terms **phenotype,** to designate individuals that look alike, and **genotype,** to designate individuals that breed alike. The tall peas of the F_2 generation constitute a phenotype which can be shown to be made up of two genotypes. On the other hand, the dwarf peas, or any individual that appears recessive, will always breed true for the recessive characteristic; the recessive phenotype is identical with the genotype.

If any dominant characteristic be represented by D and any recessive characteristic by d, the following summary of the possible crosses can be made.

(Parents) $DD \times DD$ 100 per cent DD (offspring)
(Parents) $dd \times dd$ 100 per cent dd (offspring)
(Parents) $DD \times dd$ 100 per cent Dd (offspring)
(Parents) $Dd \times Dd$ 25 per cent DD plus 50 per cent Dd plus 25 per cent dd (offspring)
(Parents) $DD \times Dd$ 50 per cent DD plus 50 per cent Dd (offspring)
(Parents) $Dd \times dd$ 50 per cent Dd plus 50 per cent dd (offspring)

It must be understood that large numbers of specific cases were studied in order to obtain the percentages that have been indicated as characteristic of these crosses. Figure 6.3 gives some of the actual numbers of individuals in the F_2 generations in Mendel's original monohybridization experiments.

Extension of Mendelian Theory. Mendel published the results of his studies in 1866, but they remained unknown until 1900, when his paper was discovered by three scientists who had independently reached the conclusions that he had stated so clearly. Since that time, his results have been confirmed by experiments with many plants and animals. For example, when a gray mouse is crossed with a white mouse, all the offspring are gray. This result indicates that gray coat color is dominant to white coat color in mice (Fig. 6.4). In the F_2 generation gray and white mice occur in the ratio of 3:1. Of the gray mice which constitute three-fourths of this F_2 generation,



Character	Number of Dominants	Number of Recessives	Ratio
Form of seed	5,474 smooth	1,850 wrinkled	2.96 to 1
Color of seed coat	6,022 yellow	2,001 green	3.01 to 1
Length of stem	787 tall	277 dwarf	2.84 to 1
Color of flowers	705 colored	224 white	3.15 to 1
Position of flowers	651 axial	207 terminal	3.14 to 1
Form of pods	882 inflated	299 constricted	2.95 to 1
Color of unripe pods	428 green	152 yellow	2.82 to 1
Total	14,949	5,010	2.98 to 1

Fig. 6.3. Data from Mendel's original experiments, from which was derived the 3 : 1 ratio characteristic of the F_2 generation in monohybridization. (From H. E. Walter, *Genetics*, copyright 1922 by The Macmillan Co., reprinted by permission.)

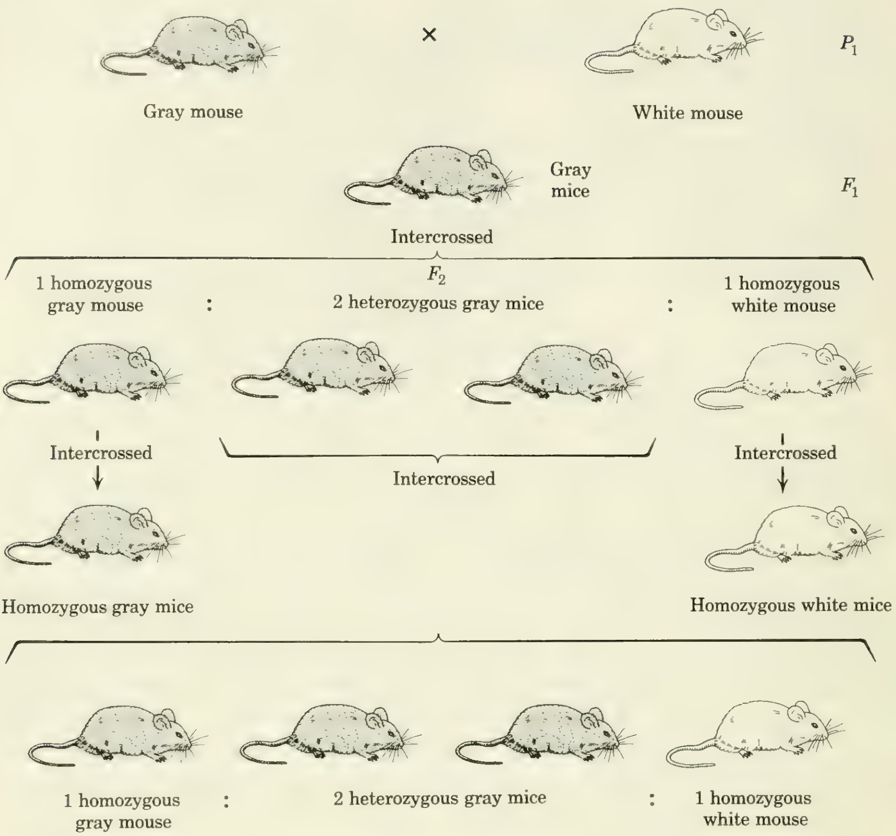

Gray mouse
×
White mouse
P_1
Gray mice
F_1
Intercrossed
F_2
1 homozygous gray mouse
:
2 heterozygous gray mice
:
1 homozygous white mouse
Intercrossed
Intercrossed
Intercrossed
Homozygous gray mice
Homozygous white mice
1 homozygous gray mouse
:
2 heterozygous gray mice
:
1 homozygous white mouse

Fig. 6.4. Results of monohybridization of mice which differ in color of coat; gray coat color is dominant to white coat color (cf. Fig. 6.11).

some are found to breed true for grayness, whereas others produce both gray and white offspring. Complete analysis by breeding reveals that 25 per cent of the F_2 generation are gray and will breed true for gray coat color, 50 per cent appear gray but will not breed true, and 25 per cent are white and reproduce only white-coated individuals when interbred.

Up to this point the examples used have involved inheritance with dominance. Dominance and recessiveness do not, however, characterize all cases of inheritance. If red and white four-o'clocks (*Mirabilis jalapa*) are crossed, the hybrids of the F_2 generation have pink flowers, not red or white. When these pink-flowered hybrids are interbred, offspring occur in the ratio of 1 red : 2 pink : 1 white. The individuals with red and white flowers breed true for these characteristic colors, whereas those with pink flowers always give three kinds of offspring in the typical 1 : 2 : 1 ratio. Another case of **inheritance without dominance** is the Blue Andalusian fowl (Fig. 6.5). Blue Andalusian fowls are produced by crossing a type of black fowl with a certain kind of white fowl. They are, therefore, hybrids and, as would be anticipated, do not breed true. Blue Andalusian parents yield 25 per cent black chicks, 50 per cent blue chicks, and 25 per cent white chicks. The black and the white offspring breed true, but the blue offspring, like all other Blue Andalusians, will always yield 25 per cent black, 50 per cent blue, and 25 per cent white individuals. The course of inheritance for characteristics that do not exhibit dominance is in no way different, therefore, from that for characteristics in which dominance occurs. In inheritance without dominance, the hybrid individuals, or those that will not breed true, can be distinguished superficially from those that will give rise to offspring like themselves. Dominance is not an essential

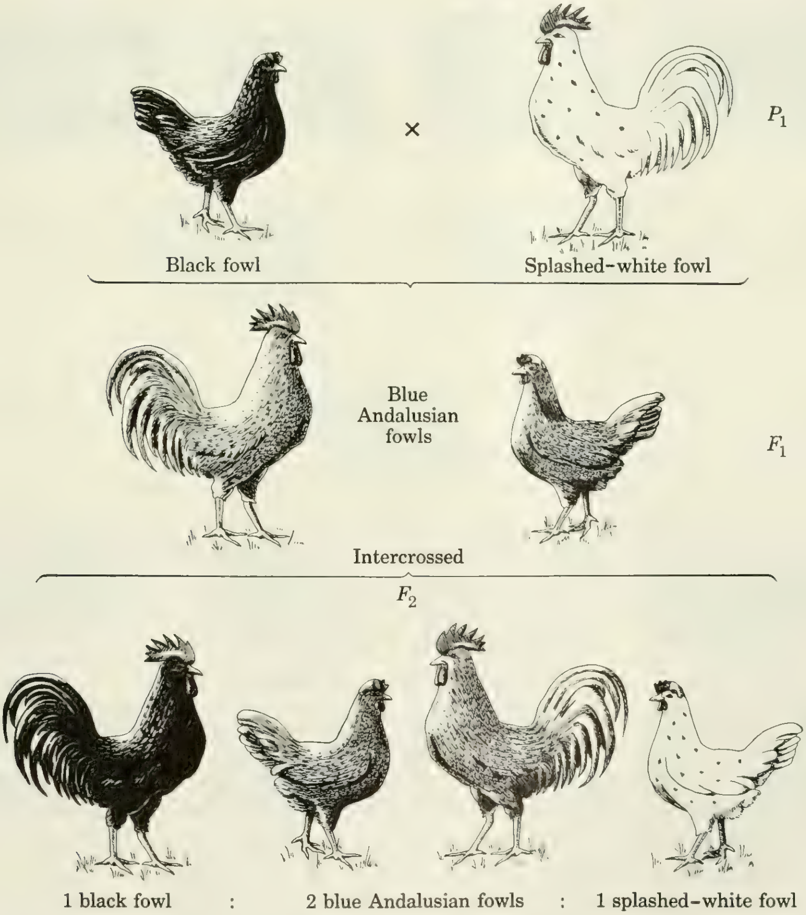

×
P_1
Black fowl
Splashed-white fowl
Blue Andalusian fowls
F_1
Intercrossed
F_2
1 black fowl : 2 blue Andalusian fowls : 1 splashed-white fowl

Fig. 6.5. Results of monohybridization of fowls which differ in color of feathers. This is an example of inheritance without dominance, since black and white parents yield blue hybrids. In the F_2 generation three visibly distinct types are produced in a 1 : 2 : 1 ratio.

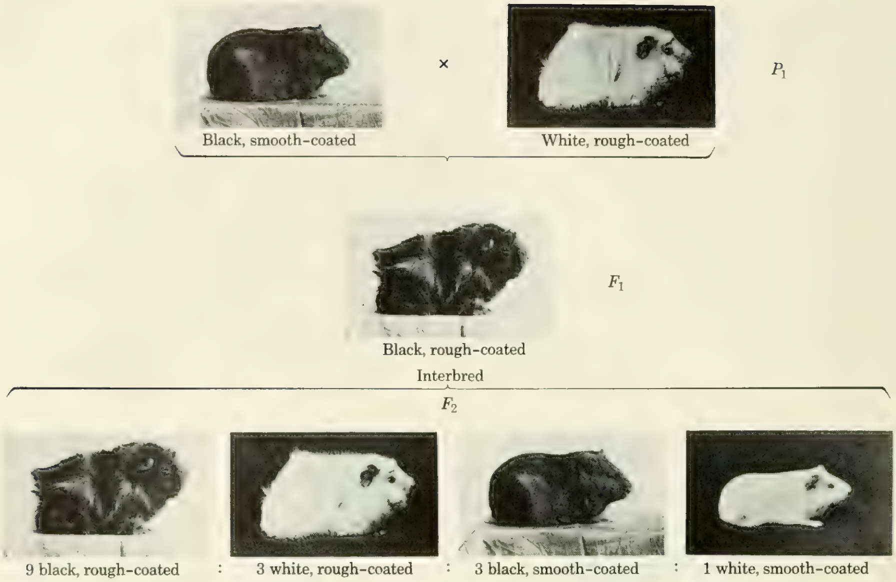


Fig. 6.6. Results of dihybridization in guinea pigs which differ in color of hair and quality of coat; black hair is dominant to white hair, and rough coat to smooth coat (cf. Fig. 6.15). (Rearrangement of figures from W. E. Castle, *Genetics and Eugenics*, copyright 1916 by Harvard University Press, printed by permission.)

feature of heredity, although it is almost universally encountered in practical breeding. The behavior of the hereditary units in the germ cells is the same whether or not dominance is involved.

If two individuals that differ in two characteristics are crossed, the process is known as **dihybridization**. In guinea pigs black hair and rough coat are dominant to white hair and smooth coat. When a black-haired, smooth-coated guinea pig is bred with a white-haired, rough-coated one, the offspring are all black-haired and rough-coated (Fig. 6.6). Whether these characteristics have been present in the male or in the female parent is not important; the combination always produces individuals in which both dominant characters are seen. When these F_1 hybrids are crossed, four kinds of offspring (phenotypes) result in the F_2 generation, in the following ratio—9 black-haired, rough-coated : 3 white-haired, rough-coated : 3 black-haired, smooth-coated : 1 white-haired, smooth-coated. Mendel's original work on dihybrids consisted in crossing wrinkled green peas with smooth yellow peas. The offspring of such a hybridization are smooth yellow peas, a fact which indicates that smooth surface is dominant to wrinkled surface and yellow color is dominant to green color in the seeds. In the F_2 generation smooth yellow peas, smooth green peas, wrinkled yellow peas, and wrinkled green peas occur in the ratio of 9 : 3 : 3 : 1.

Trihybridization is the crossing of two individuals differing in three characteristics. A third character that can be used in guinea pigs is length of hair, short hair being dominant to long hair. When a black, short-haired, smooth-coated guinea pig is crossed with a white, long-haired, rough-coated guinea pig, all the offspring of the F_1 generation are black, short-haired, and rough-coated (Fig. 6.7). Eight different kinds of individuals (phenotypes) are produced in the F_2 generation, in the ratio indicated—27 black, short-haired, rough-coated : 9 black, short-haired, smooth-coated : 9 white, short-haired, rough-coated : 9 black, long-haired, rough-coated : 3 white, short-haired, smooth-coated : 3 black, long-haired, smooth-coated : 3 white, long-haired, rough-coated : 1 white, long-haired, smooth-coated.

In the crosses previously considered, the sex of the parent having a particular characteristic has been of no significance. There are, however, cases of **sex-linked inheritance** in which the sex of the parent that possesses a certain character modifies its distribution in the offspring. Extensive work in experimental breeding for the study of heredity and variation was first carried on in this country by T. H. Morgan (Fig. 6.8) and his students, who used the

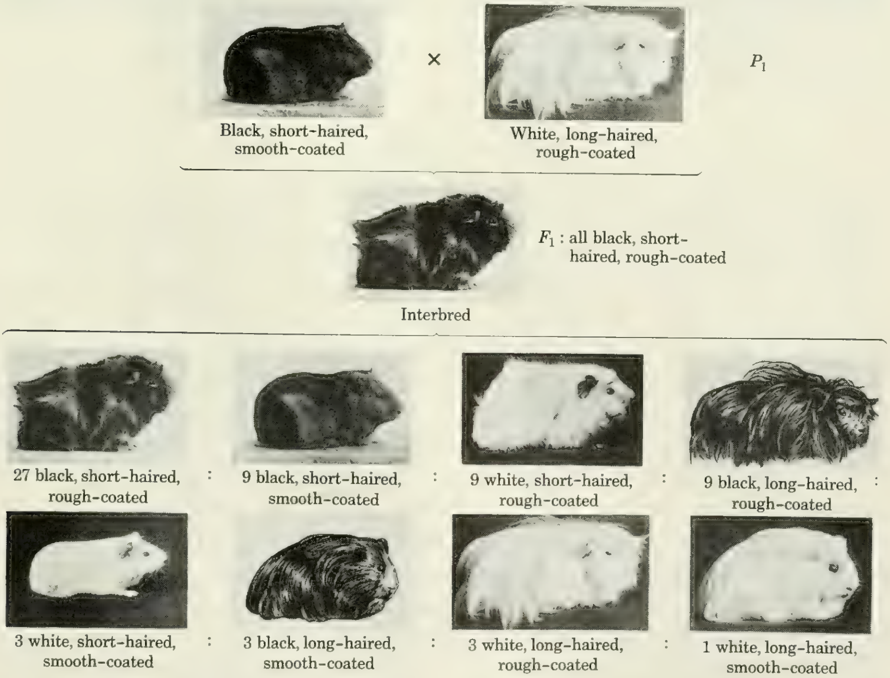

Black, short-haired, smooth-coated
×
White, long-haired, rough-coated
P_1
F_1 : all black, short-haired, rough-coated
Interbred
27 black, short-haired, rough-coated
:
9 black, short-haired, smooth-coated
:
9 white, short-haired, rough-coated
:
9 black, long-haired, rough-coated
:
3 white, short-haired, smooth-coated
:
3 black, long-haired, smooth-coated
:
3 white, long-haired, rough-coated
:
1 white, long-haired, smooth-coated

Fig. 6.7. Results of trihybridization in guinea pigs which differ in color and length of hair and quality of coat; black hair is dominant to white hair, short hair to long hair, and rough coat to smooth coat. (Rearrangement of figures from W. E. Castle, *Genetics and Eugenics*, copyright 1916 by Harvard University Press, printed by permission.)

Fig. 6.8. *Left*, Edmund Beecher Wilson, 1856–1939. *Right*, Thomas Hunt Morgan, 1866–1945. (Photographs courtesy Mrs. A. F. Huettner.)

fruit fly, *Drosophila*. An example of sex-linked inheritance may be selected from the abundant data concerning heredity in this small insect. Red eye color is dominant to white eye color in *Drosophila* (Fig. 6.9). When a red-eyed female is crossed with a white-eyed male, both male and female offspring of the F_1 generation are red-eyed. If such red-eyed individuals are intercrossed, all the females and one-half of the males of the F_2 generation have red eyes, whereas one-half of the males have white eyes. The reciprocal cross, or the cross between a white-eyed female and a red-eyed male, gives very different results (Fig. 6.10). The males of the F_1 generation are white-eyed, and the females are red-eyed. In the F_2 generation red-eyed and white-eyed males and females occur in equal numbers. When the mechanism of inheritance is considered in the following section, sex-linked inheritance will be found to furnish additional confirmation of Mendelian principles.

The method of experimental breeding, first carefully used by Mendel, has yielded a vast amount of detailed information concerning the course of inheritance of specific characteristics by particular individuals through successive generations. It was clear to Mendel that the reproductive cells, which do not, of course, exhibit the characters of stems and seeds, must carry something correlated with the appearance of characters of the adult organism from generation to generation. These "somethings" are usually called **hereditary**

factors, or genes. Mendel proved that a factor related to a specific expression of a character, such as dwarf stem, was not altered by association with a factor for the alternate expression of that character, such as long stem. Hereditary factors for the alternate or allelomorphic states in which characters are found to exist retain their unmodified independence even when present together in

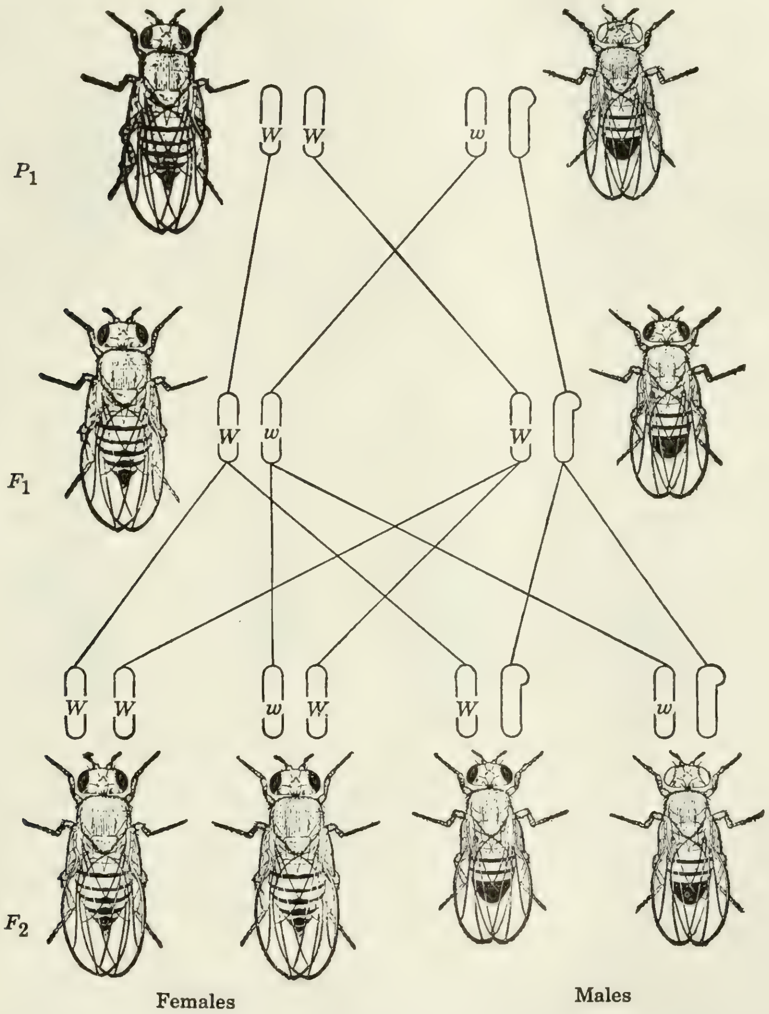


Fig. 6.9. Results of crossing a red-eyed female *Drosophila* with a white-eyed male. The X-chromosomes are represented as carriers of the genes determining eye color; *W* is the symbol used for the gene for red eye color which is dominant to the gene, indicated by *w*, for white eye color (cf. Fig. 6.17). The hook-shaped chromosome which does not contain a symbol for a gene represents the Y-chromosome of the male (cf. p. 209). This cross is the reciprocal of that shown in Fig. 6.10. (Modified from T. H. Morgan *et al.*, *The Mechanism of Mendelian Heredity*, copyright 1922 by Henry Holt and Co., printed by permission.)

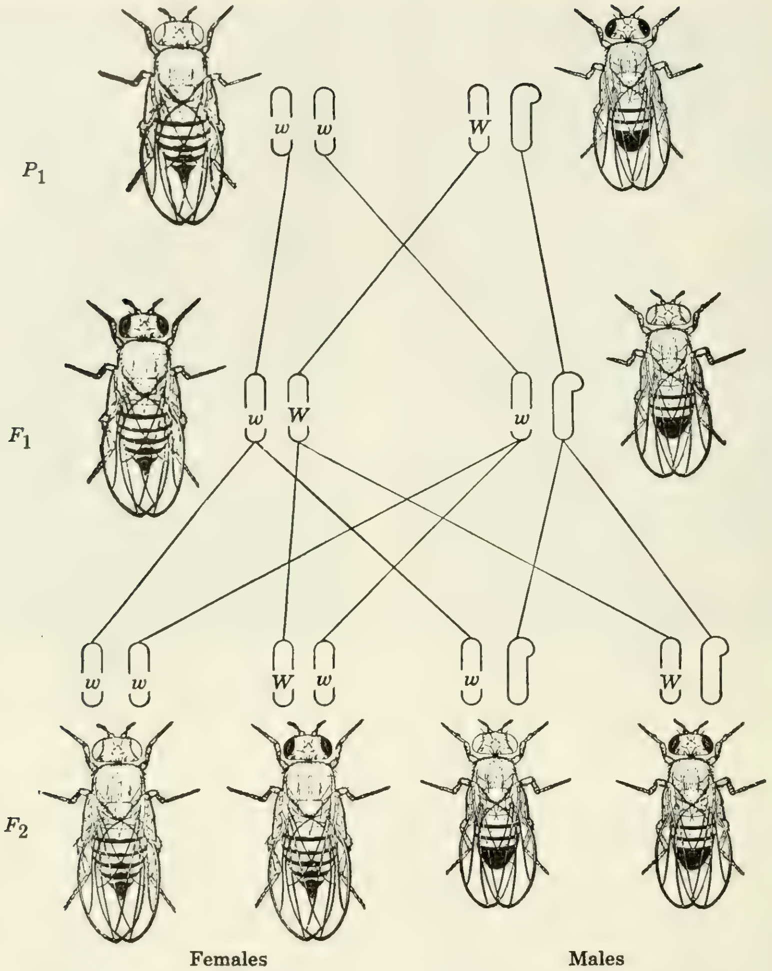


Fig. 6.10. Results of crossing a white-eyed female *Drosophila* with a red-eyed male (cf. Fig. 6.18). The X-chromosomes and the symbols for the genes are explained in the legend of Fig. 6.9, which shows the reciprocal of this cross. (Modified from T. H. Morgan *et al.*, *The Mechanism of Mendelian Heredity*, copyright 1922 by Henry Holt and Co., printed by permission.)

the cells of a hybrid individual and even though one factor is without effect in the presence of the other. When a hybrid produces its reproductive cells, these two **allelomorphic factors,** or **alleles,** one for each of the visible expressions of the character under consideration, must be able to **undergo segregation** from one another and occur alone in different reproductive cells. When **random combination** of gametes occurs to form individuals of the next generation, new combinations of genes occur which condition the characteristic ratios of mono-, di-, and trihybridization experiments. The details of the behavior of the genes can be understood best if considered in connection with that of the chromosomes.

The Method of Cytology

Chromosomes as Carriers of the Genes. When Mendel's work was brought to light in 1900, it was well known that new individuals developed from zygotes formed by the union of ova and spermatozoa. These gametes, or mature germ cells, carry the haploid number of chromosomes that is characteristic of the species; the diploid number is restored in the zygote (pp. 136 and 143). As mitosis occurs during development of the zygote, the chromosomes are distributed equally to all the cells of the new animal (p. 43). The primordial germ cells of any individual contain chromosomes that can be grouped in pairs of similar size and shape. One member of each pair is of paternal and the other of maternal origin (see Fig. 5.7, p. 135). When the first meiotic division occurs, homologous chromosomes disjoin and pass into different cells. This disjunction does not involve the separation of the sets of chromosomes that came from the two parents at the time of fertilization. On the contrary, the distribution of homologous chromosomes is random, with the members of each pair of chromosomes separating independently. These facts were discovered by the microscopical examination of germ cells by the methods of cytology. In 1902 W. S. Sutton called attention to the behavior of the chromosomes as furnishing a cellular mechanism for the explanation of Mendel's results. Since that time the theory of the chromosomes as carriers of the genes has been greatly extended, and chromosomes are now considered to be the physical basis of heredity. The researches of E. B. Wilson (Fig. 6.8) and Nettie M. Stevens in 1905–1906 were important in the analysis of the numbers and types of chromosomes in male and female animals; the work of Eleanor E. Carothers in 1917 furnished evidence for the **independent assortment** of homologous chromosomes during the meiotic divisions.

If the example of monohybridization between a gray and a white mouse is analyzed according to the concept that the genes are located in the chromosomes, the assumption is made that the zygote from which the gray mouse developed contained two genes for grayness, one from each of its parents, whereas the zygote from which the white mouse developed contained two genes for whiteness, one from each of its parents (Fig. 6.11). Each of these genes is regarded as being located in a separate chromosome, but the two genes of each animal are present in homologous chromosomes. When separation of the homologous chromosomes occurs at the disjunctional division during meiosis, the genes are carried into different gametes. All the gametes of the gray parent possess a single gene for gray coat color, and those of the white parent a single gene for white coat color. When fertilization occurs, each zygote obtains two genes for coat color, but one is for whiteness and one for grayness; the allelomorphic genes are now together in

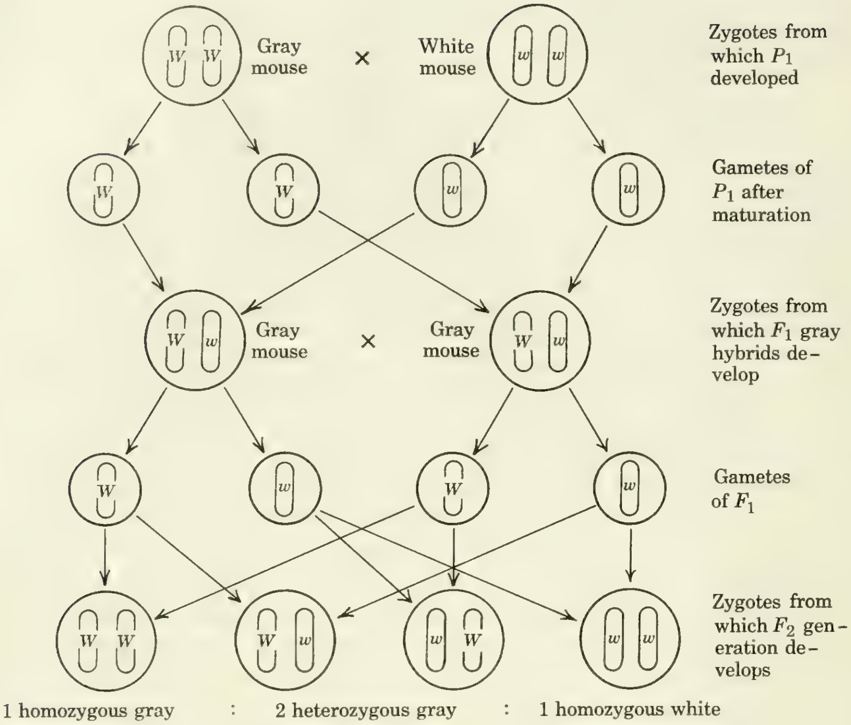

W W
Gray mouse
×
White mouse
w w
Zygotes from which P_1 developed
W
W
w
w
Gametes of P_1 after maturation
W w
Gray mouse
×
Gray mouse
W w
Zygotes from which F_1 gray hybrids develop
W
w
W
w
Gametes of F_1
W W
W w
w W
w w
Zygotes from which F_2 generation develops
1 homozygous gray : 2 heterozygous gray : 1 homozygous white

Fig. 6.11. A cross between a homozygous gray mouse and a homozygous white mouse (cf. Fig. 6.4). The diagram illustrates the segregation of a pair of genes when their carriers, a pair of homologous chromosomes, undergo disjunction; notice the possible combinations that can occur between gametes. *W*, gene for gray coat color; *w*, gene for white coat color.

the same zygote. A zygote of this kind is called a **heterozygote**, in contrast to the zygotes like those from which the parents developed, which are known as **homozygotes** because the genes of the pair are alike. The F_1 individuals are spoken of as **heterozygous**, and the parents in this case are called **homozygous**. As can be seen from Figure 6.11, two kinds of gametes are formed when disjunction occurs in individuals of the F_1 generation, and three kinds of combinations of gametes with chromosomes and genes are possible in the F_2 generation. According to chance, one of these classes, the *Ww* combination, will occur twice as frequently as either the *WW* or the *ww*. The effect of the dominance of the gene for grayness is such that both homozygous and heterozygous gray mice look alike; the apparent or phenotypic ratio in the F_2 generation is 3 gray : 1 white. It is necessary, therefore, to obtain offspring from particular crosses in order to differentiate genetically between individuals that exhibit a dominant characteristic, that is, to separate the genotypes of the dominant phenotype. The theoretical explanation of the results obtained when a heterozygous gray mouse is crossed with a white

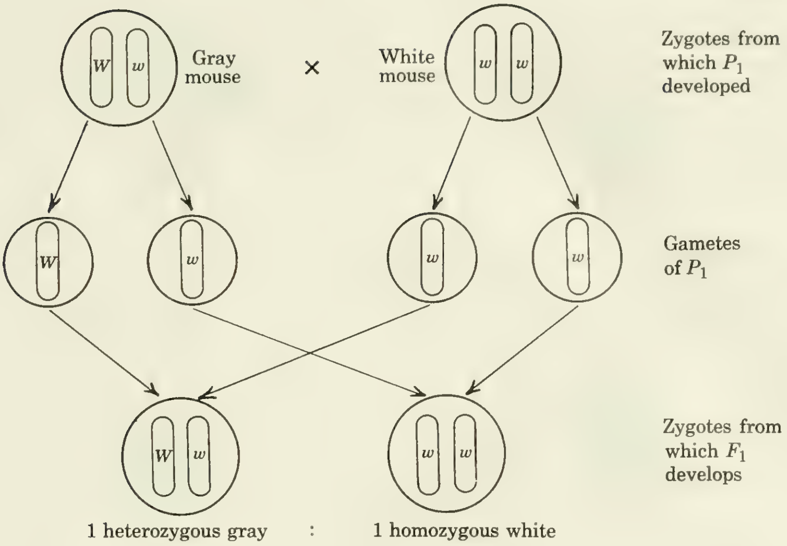

W
w
Gray mouse
×
White mouse
w
w
Zygotes from which P_1 developed
W
w
w
w
Gametes of P_1
W
w
w
w
Zygotes from which F_1 develops
1 heterozygous gray : 1 homozygous white

Fig. 6.12. A cross between a heterozygous gray mouse and a homozygous white mouse. The diagram illustrates the segregation of a pair of genes when their carriers, a pair of homologous chromosomes, undergo disjunction; notice the possible combinations that can occur between gametes. *W*, gene for gray coat color; *w*, gene for white coat color.

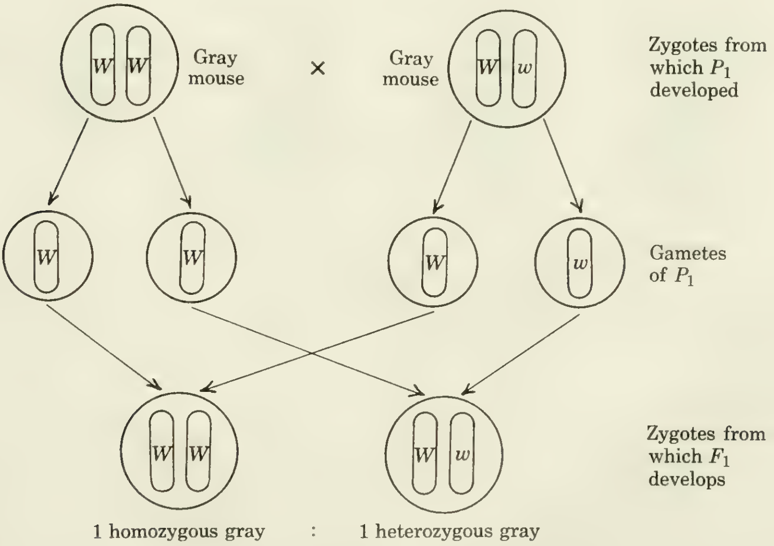

W
W
Gray mouse
×
Gray mouse
W
w
Zygotes from which P_1 developed
W
W
W
w
Gametes of P_1
W
W
W
w
Zygotes from which F_1 develops
1 homozygous gray : 1 heterozygous gray

Fig. 6.13. A cross between a homozygous gray mouse and a heterozygous gray mouse. The diagram illustrates the segregation of a pair of genes when their carriers, a pair of homologous chromosomes, undergo disjunction; notice the possible combinations that can occur between gametes. *W*, gene for gray coat color; *w*, gene for white coat color.

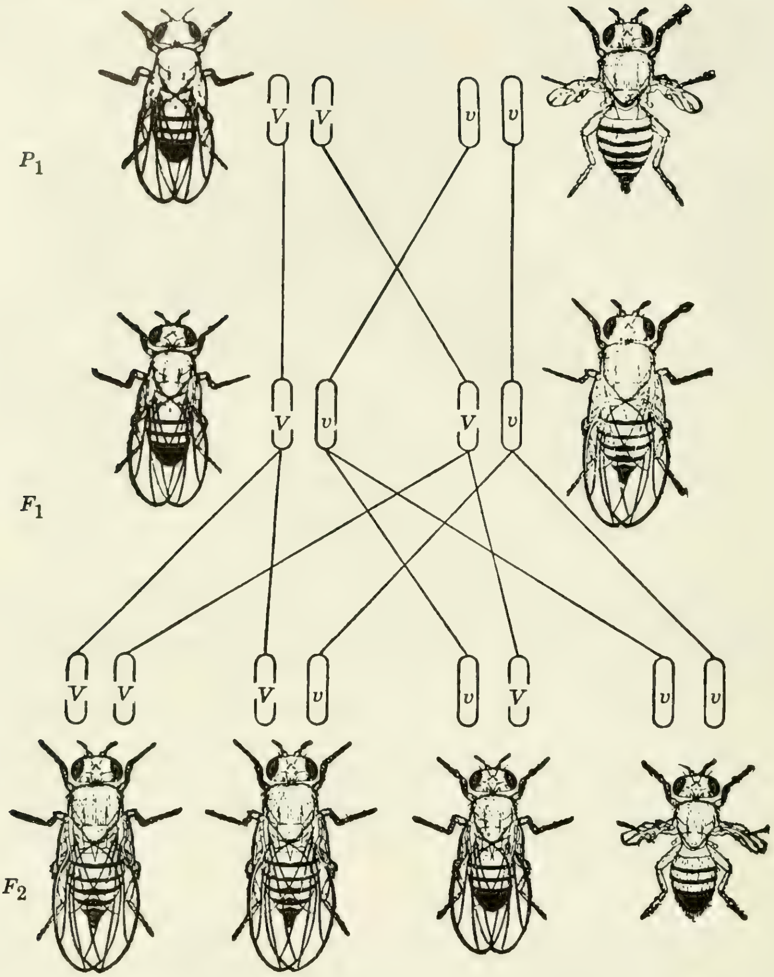
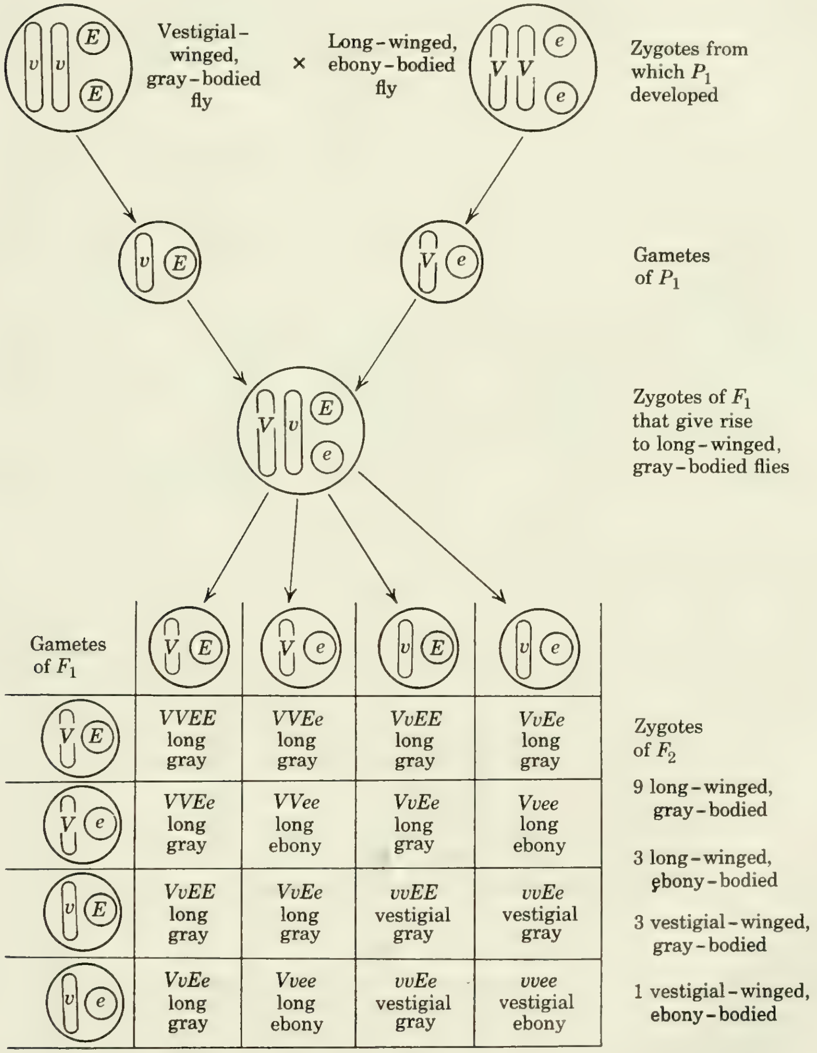


Fig. 6.14. Results of monohybridization of flies which differ in type of wing. The chromosomes are shown as the carriers of the genes; *V* is the symbol used for the gene for long wing, which is dominant to the gene, *v*, for vestigial wing (cf. Fig. 6.11). (Modified from T. H. Morgan *et al.*, *The Mechanism of Mendelian Heredity*, copyright 1922 by Henry Holt and Co., printed by permission.)

mouse, which will always be homozygous since white is recessive, is presented in Figure 6.12. This is known as a **back-cross with a recessive.** The difference between the offspring obtained in this cross and those obtained by crossing a homozygous gray with a white mouse (Fig. 6.11) furnishes the type of breeding test used for differentiating homozygous from heterozygous dominant individuals. The diagram in Figure 6.13 shows why indiscriminate crossing between the gray mice would fail to yield information that would enable one to distinguish homozygous gray mice with certainty. In the case illustrated all the offspring will be gray in both the F_1 and F_2 generations; the same situation would prevail if both original gray mice had been homozygous. However, if any white mice appeared in a cross between two grays, their presence would prove both parents to be heterozygous.

The breeding results are explained adequately in these cases of mono-


v v E E
Vestigial-winged, gray-bodied fly
×
Long-winged, ebony-bodied fly
V V e e
Zygotes from which P_1 developed
v E
V e
Gametes of P_1
V v E e
Zygotes of F_1 that give rise to long-winged, gray-bodied flies
Zygotes of F_2
9 long-winged, gray-bodied
3 long-winged, ebony-bodied
3 vestigial-winged, gray-bodied
1 vestigial-winged, ebony-bodied

Gametes of F_1	V E	V e	v E	v e
V E	*VVEE* long gray	*VVEe* long gray	*VvEE* long gray	*VvEe* long gray
V e	*VVEe* long gray	*VVee* long ebony	*VvEe* long gray	*Vvee* long ebony
v E	*VvEE* long gray	*VvEe* long gray	*vvEE* vestigial gray	*vvEe* vestigial gray
v e	*VvEe* long gray	*Vvee* long ebony	*vvEe* vestigial gray	*vvee* vestigial ebony

Fig. 6.15. A case of dihybridization between a vestigial-winged, gray-bodied fly (*Drosophila*) and a long-winged, ebony-bodied fly (cf. Fig. 6.6). The diagram illustrates disjunction and independent assortment of two pairs of homologous chromosomes which carry two pairs of genes; notice the possible combinations that can occur between the gametes formed. *E*, gene for gray body; *e*, gene for ebony body; *V*, gene for long wing; *v*, gene for vestigial wing.

hybridization by the assumption that allelomorphic genes conditioning the alternate expressions of the character used are carried in homologous chromosomes and thus distributed to gametes and zygotes (Fig. 6.14). The theory of the chromosomes as the physical basis of heredity can also be used to explain cases of di- and trihybridization. In *Drosophila* long wing (V) is dominant to short or vestigial wing (v), and gray body color (E) is dominant to ebony (e) body color. A fly with vestigial wings and gray body ($vvEE$) is mated with a long-winged fly with ebony body ($VVee$) (Fig. 6.15). At the time of the first meiotic division the homologous chromosomes of each pair undergo disjunction and pass into different gametes. The gametes produced by the parents contain genes vE and Ve, respectively. The zygotes of the F_1 generation will be $VvEe$ and will develop into long-winged, gray-bodied flies. Four different kinds of gametes can be formed by these F_1 individuals, since the different pairs of homologous chromosomes assort independently when they undergo disjunction at the first meiotic division. Segregation and independent assortment of genes yield the following four classes of gametes in any F_1 individual: VE, Ve, vE, and ve. Random combination of gametes containing such genes gives rise to 16 possible zygotes that develop into the F_2 generation as shown in the checkerboard at the bottom of Figure 6.15. There are four phenotypes occurring in a 9 : 3 : 3 : 1 ratio and nine genotypes ($VVEE$, $VVEe$, $VvEE$, $VvEe$, $VVee$, $Vvee$, $vvEE$, $vvEe$, and $vvee$).

Linkage. The discussion of the chromosomes as the carriers of the genes has been concerned so far with what could occur if each gene were carried in a separate chromosome. It was discovered by W. Bateson and R. C. Punnett in 1906 that certain characteristics were linked in inheritance. They found, in crossing a sweet pea with purple flowers and long pollen grains and a sweet pea with red flowers and round pollen grains, that the genes which came from each parent tended to remain together instead of assorting independently during meiosis. The study of inheritance of several hundred genes in *Drosophila* shows that they fall into four groups; the genes composing each of these groups are said to be **linked** (Fig. 6.16). Cytological investigation demonstrates the presence of four pairs of chromosomes in *Drosophila* (see Fig. 2.12*D* and *E*, p. 42), and pairs of linked genes are known to be carried by pairs of homologous chromosomes. Furthermore, there is evidence which is interpreted to indicate that genes in a chromosome are arranged like beads on a string, and relative distances between genes in the string have been computed (Fig. 6.16). This **linear order** of the genes makes the longitudinal reduplication of the chromosomes and subsequent separation of the sister genonemata highly significant events (p. 43).

The example of sex-linked inheritance described as a breeding experiment (p. 181) can be explained if it be assumed that the X-chromosomes carry the genes concerned with red and white eye color. It will be recalled that in the cells of a female there are two so-called X-chromosomes, whereas in the male only one X-chromosome is found (see Fig. 2.12*D* and *E*, p. 42) The male *Drosophila* possesses one X-chromosome and a Y-chromosome which car-

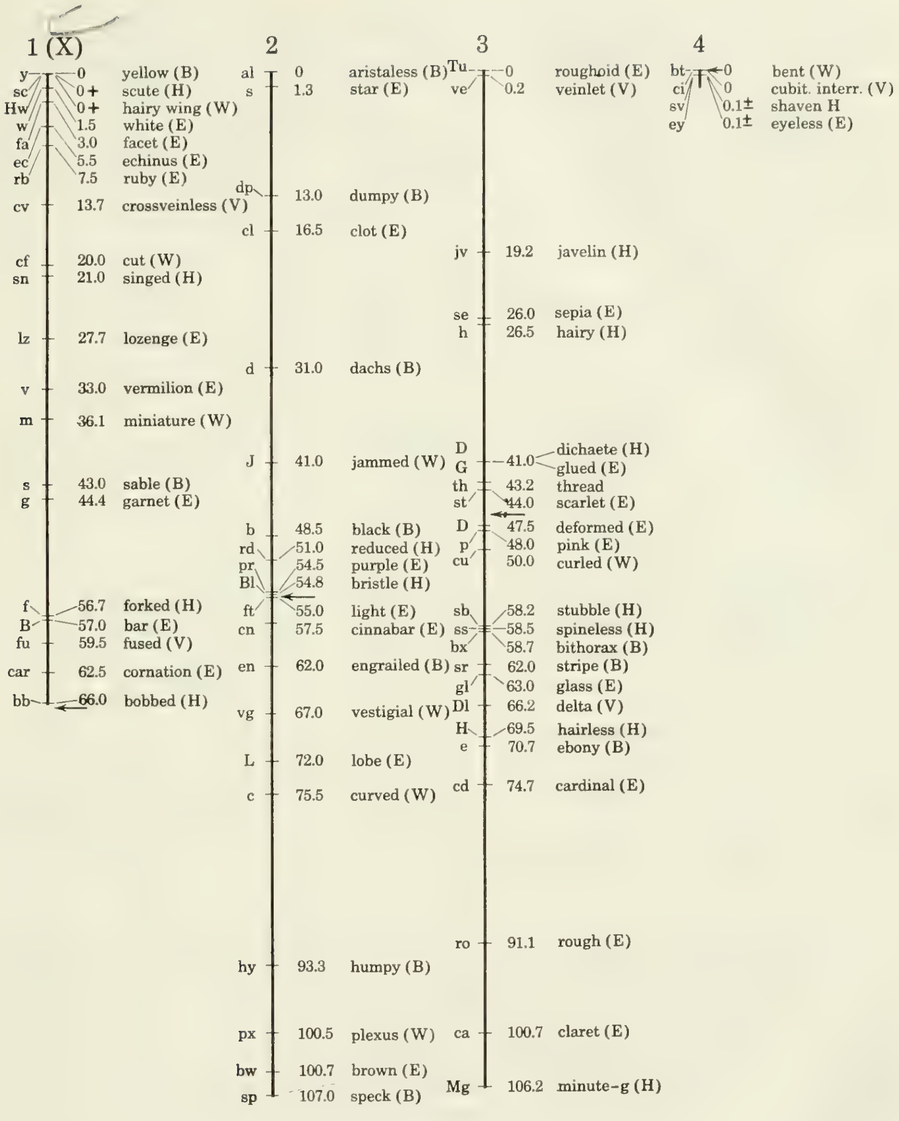

1 (X)
y 0 yellow (B)
sc 0+ scute (H)
Hw 0+ hairy wing (W)
w 1.5 white (E)
fa 3.0 facet (E)
ec 5.5 echinus (E)
rb 7.5 ruby (E)
cv 13.7 crossveinless (V)
cf 20.0 cut (W)
sn 21.0 singed (H)
lz 27.7 lozenge (E)
v 33.0 vermilion (E)
m 36.1 miniature (W)
s 43.0 sable (B)
g 44.4 garnet (E)
f 56.7 forked (H)
B 57.0 bar (E)
fu 59.5 fused (V)
car 62.5 cornation (E)
bb 66.0 bobbed (H)
2
al 0 aristaless (B)
s 1.3 star (E)
dp 13.0 dumpy (B)
cl 16.5 clot (E)
d 31.0 dachs (B)
J 41.0 jammed (W)
b 48.5 black (B)
rd 51.0 reduced (H)
pr 54.5 purple (E)
Bl 54.8 bristle (H)
ft 55.0 light (E)
cn 57.5 cinnabar (E)
en 62.0 engrailed (B)
vg 67.0 vestigial (W)
L 72.0 lobe (E)
c 75.5 curved (W)
hy 93.3 humpy (B)
px 100.5 plexus (W)
bw 100.7 brown (E)
sp 107.0 speck (B)
3
Tu 0 roughoid (E)
ve 0.2 veinlet (V)
jv 19.2 javelin (H)
se 26.0 sepia (E)
h 26.5 hairy (H)
D 41.0 dichaete (H)
G 41.0 glued (E)
th 43.2 thread
st 44.0 scarlet (E)
D 47.5 deformed (E)
p 48.0 pink (E)
cu 50.0 curled (W)
sb 58.2 stubble (H)
ss 58.5 spineless (H)
bx 58.7 bithorax (B)
sr 62.0 stripe (B)
gl 63.0 glass (E)
Dl 66.2 delta (V)
H 69.5 hairless (H)
e 70.7 ebony (B)
cd 74.7 cardinal (E)
ro 91.1 rough (E)
ca 100.7 claret (E)
Mg 106.2 minute-g (H)
4
bt 0 bent (W)
ci 0 cubit. interr. (V)
sv 0.1± shaven H
ey 0.1± eyeless (E)

Fig. 6.16. Maps of the four chromosomes of the haploid set in *Drosophila;* the genes located in any one chromosome and their allelomorphs constitute a linkage group. Chromosome 1 is the X-chromosome, and 4 is the small round one (cf. Fig. 2.12*D*, p. 42, and Fig. 6.19*A*). Letters in parentheses indicate part of fly where effect of mutant gene is observed: *B*, body; *E*, eyes; *H*, bristles; *V*, venation of wings; *W*, wings. The positions of association with the spindle (cf. p. 41) are indicated by arrows. (After C. Bridges, from A. H. Sturtevant and G. W. Beadle, *An Introduction to Genetics*, copyright 1939 by W. B. Saunders Co., printed by permission.)

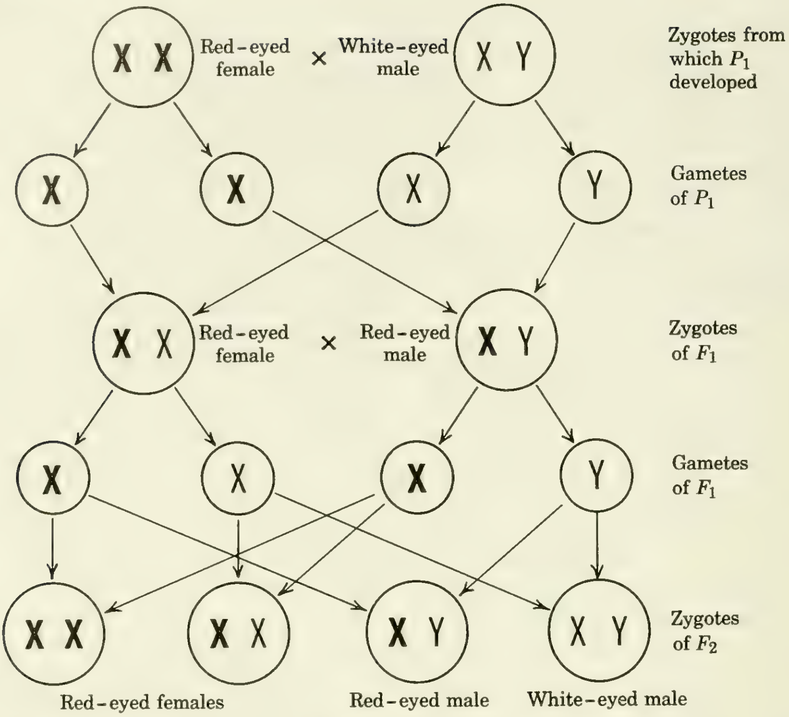

X X
Red-eyed female
×
White-eyed male
X Y
Zygotes from which P_1 developed
X
X
X
Y
Gametes of P_1
X X
Red-eyed female
×
Red-eyed male
X Y
Zygotes of F_1
X
X
X
Y
Gametes of F_1
X X
X X
X Y
X Y
Zygotes of F_2
Red-eyed females
Red-eyed male
White-eyed male

Fig. 6.17. A cross between a red-eyed female *Drosophila* and a white-eyed male (cf. Fig. 6.9). The diagram illustrates disjunction of sex chromosomes during the formation of gametes and the possible combinations of these; the X-chromosomes carry genes for eye color. This is the reciprocal of the cross shown in Figure 6.18. **X,** X-chromosome carrying gene for red eye color; X, X-chromosome carrying gene for white eye color; Y, Y-chromosome which is confined to males and does not carry a gene for eye color.

ries very few genes and does not leave the male line. Each ovum formed during maturation contains one X-chromosome; one-half of the sperm have an X-chromosome, the other half have a Y-chromosome. In the cross between a homozygous red-eyed female *Drosophila* and a white-eyed male, each ovum contains an X-chromosome carrying a gene for red eye color, whereas half the sperm have an X-chromosome bearing a gene for white eye color and half have a Y-chromosome which has no gene for eye color (Fig. 6.17). Random unions of ova and spermatozoa result in red-eyed females and red-eyed males in the F_1 generation. The females are red-eyed because the gene for red eye color is dominant to the gene for white eye color. These females are, however, heterozygous for eye color and give rise to two kinds of ova, in one of which the X-chromosome carries a gene for red eye color, and in the other the X-chromosome carries a gene for white eye color. Half the spermatozoa produced by the red-eyed males have an X-chromosome with a gene for red eye color and half have the Y-chromosome. Combinations of the gametes in a cross between a male and a female of the F_1 generation result in red-eyed females, red-eyed males, and white-eyed males. In this kind of inheritance the white-eyed characteristic of the male parent does not occur in the F_1 generation but reappears in one-half the males of the F_2 generation. The reciprocal cross, in which a white-eyed female is mated with a red-eyed male, is shown in Figure 6.18. If the distribution of the X-chromosomes is followed, the reason for the difference between the offspring from these two crosses should be clear. It is to be understood that sex linkage is not an exception to Mendelian principles but confirms the theory that chromosomes carry the genes.

Cytology has furnished knowledge of the behavior of chromosomes and their transmission from one generation to the next. The experimental breeder has been able to explain adequately the results obtained in his breeding experiments by the assumption that what is present in the zygote and determines the appearance of a character in an adult organism is carried by the chromosomes. These hypothetical determiners of inherited characters are known as

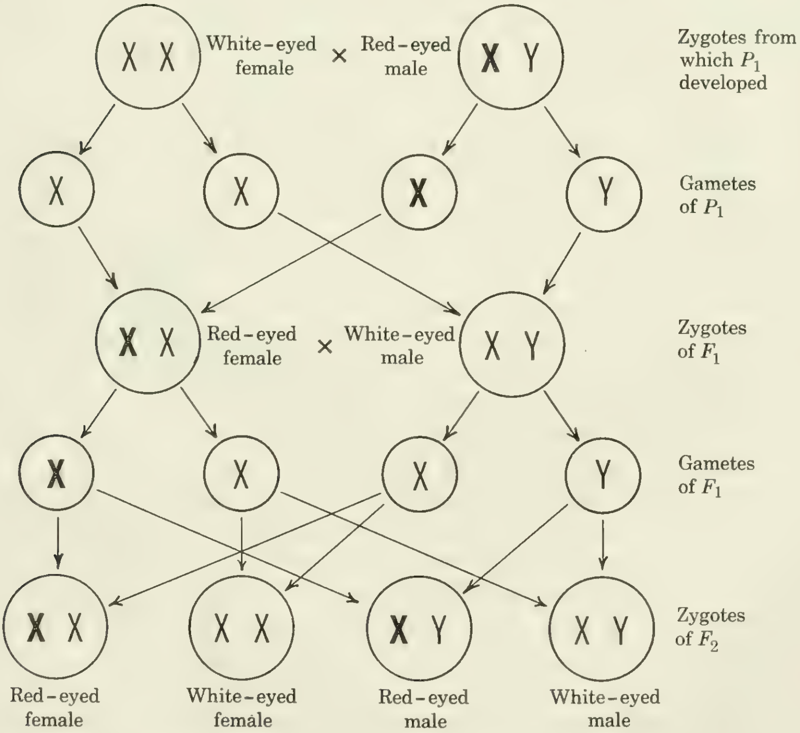

X X
White-eyed female
×
Red-eyed male
X Y
Zygotes from which P_1 developed
X
X
X
Y
Gametes of P_1
X X
Red-eyed female
×
White-eyed male
X Y
Zygotes of F_1
X
X
X
Y
Gametes of F_1
X X
X X
X Y
X Y
Zygotes of F_2
Red-eyed female
White-eyed female
Red-eyed male
White-eyed male

Fig. 6.18. A cross between a white-eyed female *Drosophila* and a red-eyed male (cf. Fig. 6.10). The diagram illustrates disjunction of sex chromosomes during the formation of gametes and the possible combinations of these; the X-chromosomes carry genes for eye color. This is the reciprocal of the cross shown in Figure 6.17, the legend of which describes the symbols.

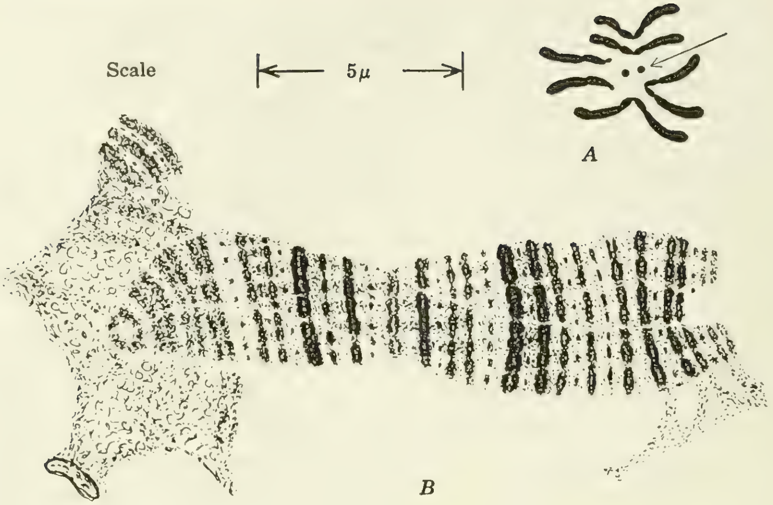


Fig. 6.19. Chromosomes of *Drosophila*. *A*, equatorial plate from an oögonium; chromosome pair IV is seen in the center of the group. *B*, chromosome pair IV from a salivary gland cell; members of each pair of chromosomes are closely associated, greatly increased in size, and exhibit conspicuous banding. (From C. B. Bridges, 1935, *Journal of Heredity*, vol. 26.)

hereditary factors, or genes. It is known that many genes are found in a single chromosome and that they are arranged in a row along the length of the gene string. In the cells of the salivary gland of *Drosophila* the chromosomes are very large because of several reduplications of the genonemata without nuclear division (Fig. 6.19). The bands on these chromosomes are characteristic and constant in position on the members of a pair which are closely associated side by side. When certain genes are found to be missing in breeding experiments, a cytological examination of these banded chromosomes reveals that certain bands are absent (Fig. 6.20); that is, the genes of a linkage group can be considered to occupy definite positions in a specific linear order on a pair of homologous chromosomes.

Genes are distributed equally by the mechanism of mitosis to all the germ cells derived from a zygote. The mechanism of disjunction and independent assortment of the pairs of homologous chromosomes, during maturation of the germ cells, and the possibilities of random combination of the germ cells furnish a cellular basis by means of which Mendelian ratios can be explained.

The Method of Experimental Embryology

Experimental breeding is usually carried on under the conditions most favorable for the organisms concerned. The results obtained, therefore, are comparable with what might be expected to occur in uncontrolled breeding in the natural habitat. This normal course of inheritance can be observed and interpreted, as has been explained. From it we learn the laws of the transmission of the hereditary units; we learn the mechanism of heredity.

How does a particular complement of genes, or **genome**, influence the course of development of a zygote in such a way as to condition the appearance of the phenotype? What is the relation of gene to character? In this, as in many fields of study, a knowledge of what happens under abnormal or unusual conditions may clarify our understanding of the normal situation. In the examples cited to illustrate Mendelian principles, a certain combination of genes always gives a certain type of individual. However, if the genetic combination remains the same but the environment is changed, the individuals may be different (p. 167). For example, the red primrose has red flowers if kept at a temperature ranging from 15° to 20°C. A plant with the same genes, reared at a temperature of 30° to 35°C. with other environmental conditions unchanged, produces white flowers. If a plant with white flowers is brought into a room at 15° to 20°C., the flowers that develop later will be red. The effect of the genes for color of flower is limited by the temperature of the environment in which the flowers develop. That the gene is not altered is shown by the ability of the plant to cease producing white flowers and give rise to red ones when kept at a different temperature (cf. Fig. 6.21). The same type of effect has been demonstrated in *Drosophila*. A certain race of the fruit fly is distinguished from the normal by the fact that there are very few black bands on the abdomen. When this race is

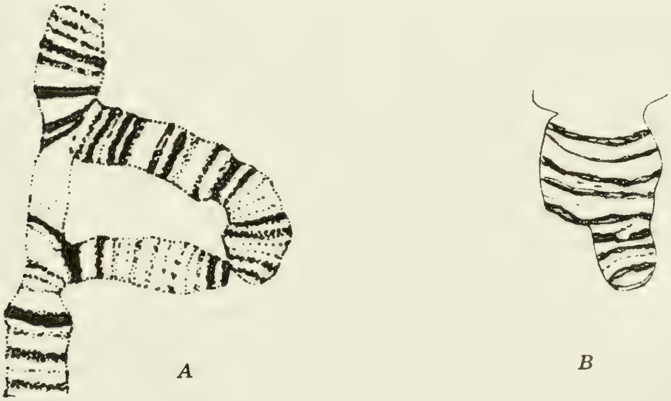


Fig. 6.20. Chromosomal aberrations seen in the paired salivary-gland chromosomes of *Drosophila*. *A*, part of the pair of X-chromosomes, one of which has lost an internal section by deletion (cf. Fig. 6.23); the bent portion of the normal partner indicates the length of the deleted section. *B*, the end of a pair of X-chromosomes, one of which has lost a terminal section. (*A*, from T. S. Painter, 1934, *Journal of Heredity*, vol. 25; *B*, from M. Demerec and Margaret E. Hoover, 1936, *Journal of Heredity*, vol. 27.)

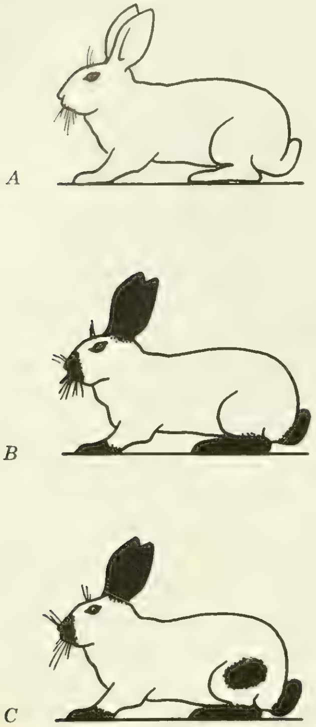


Fig. 6.21. The appearance of Himalayan rabbits under different temperature conditions. *A*, a rabbit raised at a temperature above 30°C. *B*, a rabbit raised at a temperature of about 25°C. *C*, a rabbit which has had its left flank artificially cooled at a temperature below 25°C. (After R. Danneel, from R. P. Wagner and H. K. Mitchell, *Genetics and Metabolism*, copyright 1955 by John Wiley and Sons, Inc., reprinted by permission.)

reared on a rich supply of moist food, the abdominal bands are almost completely absent in all individuals. The same stock raised on scant, dry food exhibits normal banding of the abdomen. If a culture is started with abundant moist food which is not replenished but allowed to become dry, the individuals that develop first will show abnormal banding, and those that develop later will appear normal. These flies are genetically the same; the difference in their appearance is conditioned by the environment in which they develop. In other words, the appearance of characters in an adult individual is dependent on the presence of certain genes in the zygote acting in a particular environment during development.

The age of an individual sometimes affects the development of characters. Certain characters may not appear until the individual reaches a particular age. In other individuals a character may appear in early stages of development and be lacking in the adult. Age is, in this sense, a phase of the environment. The relationship between genes and environment is shown further by the fact that in *Drosophila* red color is confined to the eyes and does not occur on the legs or wings. The influence of genes is likewise dependent on their association with certain other genes; evidence for the interaction of genes is clear-cut but very complicated and will not be given here. At least 25 pairs of allelomorphic genes are concerned with eye color in *Drosophila*. Conversely, a single pair of genes may influence more than one character. In *Drosophila* the genes for rudimentary wings affect characters of the legs and the number of eggs laid.

Genes are the functional units that determine inheritance in organisms. At least two allelomorphic genes can be associated with the appearance of each heritable character of an individual. In many instances it is known that three or more allelic states of the gene for a particular character exist. No more than two of these **multiple allelomorphs** are present in a particular individual. There may be many pairs of allelomorphic genes that interact to produce a given character. A single pair of genes may also influence the appearance of more than one character. Certain environmental factors during development of a character limit the effect of the genes.

Microorganisms such as bacteria and molds are now widely used in studies concerning the nature of the gene and the way in which hereditary factors produce their effects; such investigations are sometimes known as **physiological genetics.** The possibility of exact control and the ease of modification of their environment, together with their rapid rate of reproduction, make these simple plants desirable material for genetic studies. This serves to point up the fact that no fundamental differences in the mechanisms of heredity and variation have been found to exist between animals and plants, unicellular or multicellular. The tentative hypothesis concerning the nature of genes proposes that they are molecules of desoxyribonucleic acid (DNA), possibly complexed with distinctive protein moieties. It should be understood that the number of structurally unique DNA molecules is, theoretically, almost unlimited, as is true of protein molecules. These distinctive chemical units, the genes, are conceived to be held together in linear order by physicochemical forces. The effects of the genes arranged in these gene strings, or genonemata, are believed to be conditioned not only by their own unique chemical structure but, also, by that of contiguous hereditary units, as well as the reactant substrate outside the chromosomes. Long chain reactions occurring between the constituents of the cytoplasm in any particular region, triggered by an enzyme produced by one particular gene and modified by enzymes formed by other genes, are thought to result in the differentiation of the hereditary characteristics of organisms. You may want to refresh your memory concerning enzyme-directed chain reactions in cells by referring again to Figure 2.9, p. 36.

Human Inheritance

Man's characteristics, determined by genes at more than 5000 loci, are inherited from generation to generation, as are those of other living organisms. The course of heredity is well understood for many characteristics, and much information has been accumulated. For the inheritance of human eye color there is a pair of genes, the dominant member of which must be

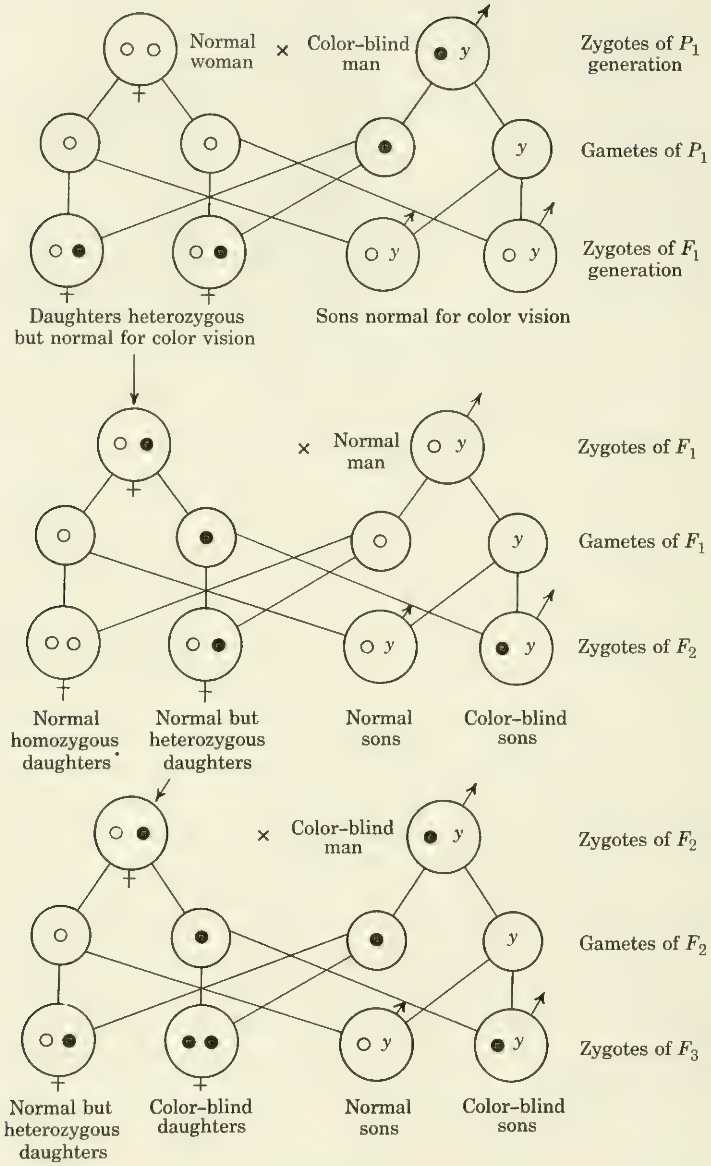

Normal woman
×
Color-blind man
Zygotes of P_1 generation
Gametes of P_1
Zygotes of F_1 generation
Daughters heterozygous but normal for color vision
Sons normal for color vision
×
Normal man
Zygotes of F_1
Gametes of F_1
Zygotes of F_2
Normal homozygous daughters
Normal but heterozygous daughters
Normal sons
Color-blind sons
×
Color-blind man
Zygotes of F_2
Gametes of F_2
Zygotes of F_3
Normal but heterozygous daughters
Color-blind daughters
Normal sons
Color-blind sons
y

Fig. 6.22. Inheritance of color blindness in man. The gene for a defective retina is located in the X-chromosome, which explains the crisscross transmission from a color-blind man to half the sons of his daughters. Color-blind daughters may occur if a woman heterozygous for color vision marries a color-blind man, as shown in the third cross. The symbol for a female is ♀; ♂ is the symbol for a male. An X-chromosome carrying a gene for normal color vision is indicated by o; ● indicates an X-chromosome carrying a gene for color blindness; *y* is the Y-chromosome of the male.

present if any pigment is to be deposited in the eye. Individuals who carry two recessive genes in their cells are albinos; their eyes appear pink because the blood vessels of the iris are not screened by pigment. Where pigment is deposited, another pair of genes conditions its distribution. Homozygous or heterozygous dominant individuals have a purple-black pigment behind the iris and brown pigment in front of the iris and appear brown-eyed. Homozygous recessive individuals have pigment only behind the iris and appear blue-eyed. The albino genes affect pigmentation of the skin and hair, as well as of the eye. Curly hair is dominant to straight hair. In color blindness, which is the result of an inherited defect of the retina, and in hemophilia, a defect of the blood that prevents its clotting, the genes are sex-linked (Fig. 6.22). The production of the A, B, M, N, and Rh antigens found in human red blood cells is determined by heredity (pp. 65 and 164). The Rh (D) gene is dominant, and individuals homozygous or heterozygous for it contain the Rh antigen. In the A and B substances we have an example of multiple allelomorphs. Three allelic genes are known to condition the blood types, but only two of these genes occur in any individual. They are symbolized as A (gives A antigen), a^B (gives B antigen), and a (gives neither antigen). Individuals may, therefore, be genotypically AA or Aa and have blood of type A; a^Ba^B or a^Ba and have blood of type B; Aa^B and have blood of type AB; aa and have blood of type O. Among individuals of European stock 45 and 42 per cent, respectively, type as O and A, only 3 per cent as AB.

Mental as well as physical characteristics appear to be inherited. The evidence seems to indicate that mental qualities leading to degeneracy, crime, and pauperism, as well as those yielding leadership in all social fields, may be inherited according to Mendelian principles. It is not to be understood that there are special genes determining crime or pauperism but rather that genes giving rise to defective mental equipment predispose to these undesirable social traits. In the same way the so-called inheritance of diseases is an inheritance of morphological or physiological characteristics that render an individual more susceptible to infections. Instances of prenatal infection (p. 164) are not cases of inheritance as the term has been used in this chapter.

The environment in which a particular gene complex develops may limit and obscure its possibilities. Thus, a given combination of genes in a human individual may produce a better adult in a favorable environment than it could in an unfavorable one. On the other hand, a good combination of genes will give rise to a better individual in a particular environment than will a poor set of genes. Training is another element that is very important in the unfolding of human potentialities. An inferior inheritance with superior training may result in an individual better fitted for society than one with a good inheritance and no training. But no amount of training can produce anything for which the inherited capacities are not present, nor can the best of environments implant qualities if the potentialities for them are lacking in the germ plasm. In other words, heredity limits very definitely the effects of training and environment.

Eugenics is that particular branch of applied genetics which deals with the improvement of the mental and physical characteristics of future generations of the human race. Its problems are: first, extension of our knowledge concerning human heredity; and, second, the education of the public in an appreciation of the meaning and application of this knowledge. The first of these problems is very difficult. A knowledge of hereditary principles is best gained from controlled and repeated experiments, which obviously cannot be carried out with human beings. Thus, the social tabu against marriages between near relatives is based on the knowledge that defective offspring result if recessive genes for undesirable traits are brought together. This, of course, can also occur in marriages between unrelated individuals. Inbreeding experiments with rats conducted by Helen Dean King for many years produced an unusually vigorous stock of animals. Animals having desirable genes in a homozygous condition will be obtained by inbreeding if the desirable genes are present in the beginning; neither defective nor desirable genes are produced by inbreeding. In 1930 H. S. Jennings, in *The Biological Basis of Human Nature*, pointed out the great handicaps of eugenics in the light of modern knowledge of genetics. The phenomenon of dominance makes heterozygous individuals appear normal, although they may transmit undesirable genes. Prevention of the breeding of the socially unfit and of those afflicted with uncontrollable physical or mental handicaps, desirable as such a measure may seem, will not eliminate the heterozygous carriers.

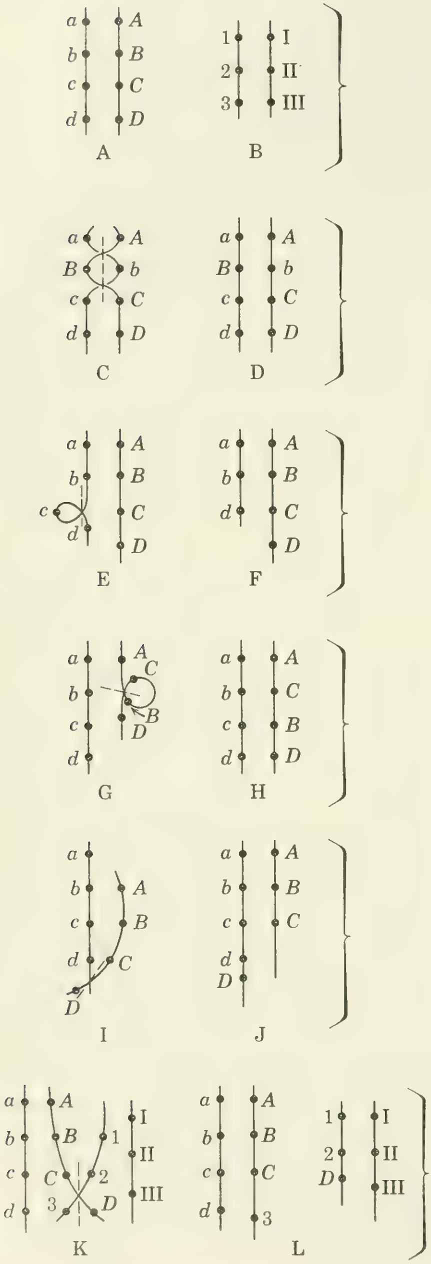
Until recently it was impossible to detect the presence of a recessive gene when it was combined with its dominant allele in a heterozygous individual, except by the breeding test. It has been found by using the technic of paper chromatography that some products of metabolism in the cells of heterozygous individuals (*Drosophila* and two species of plants) differ from those occurring in homozygous individuals. In paper chromatography, substances in solution are spot-dried on special grades of filter-type paper. Later, components of these substances can be separated from one another by allowing special liquids to move slowly through the paper. The dried substances redissolve and migrate during the movement of the fluid. Different chemical compounds are found to move at different rates and, thus separated, can be identified by various methods on the redried paper. By using this technic, it is possible to distinguish between fruit flies, for example, homozygous for certain genes and those that are heterozygous. That is, the products of metabolism in the cells of heterozygous individuals differ from those formed in homozygous individuals; these compounds migrate at different rates in the paper. Similar technics have been used successfully to identify children carrying hereditary factors that bring about a fatal blood disease (familial primary systemic amyloidosis) in adults 30 to 40 years of age, long before there is any clinical indication of the disease. If these technics for the detection of carriers can be extended, they will prove to be of revolutionary importance in the formulation of a sound program of eugenics.

Heritable Variations

The genetic data so far presented indicate two general reasons why offspring are not exactly like their parents. In the first place, the environment may influence the developing young and produce a fluctuation, or somatic variation. As was pointed out in connection with Johannsen's studies on beans (p. 174), such variations are not inherited; they do not affect the germ cells. In the second place, the results of hybridization experiments show that new combinations of genes give rise to individuals differing from their parents. Disjunction and independent assortment of the pairs of chromosomes containing the linked genes of the several groups give rise to gametes different in their genic content. The random combination of gametes to form zygotes can produce a great number of phenotypes and more genotypes in cases where dominance occurs. The possibilities of new combinations of linkage groups are limited, however, by chance, and the same variations are produced many times. This sort of thing is sometimes said to be like dealing hands of cards. Many combinations can be dealt, but the cards themselves, which would be comparable to the chromosomes carrying groups of genes, remain unchanged and occur in the same numbers and kinds.

New combinations of genes may also arise as a result of changes brought about in any linkage group by the process of **crossing over.** Crossing over happens when comparable regions of homologous chromosomes become exchanged (Fig. 6.23*C* and *D*) and gives rise to unexpected classes of offspring. If a male *Drosophila* with white eyes and a yellow body is mated to a female with red eyes and a gray body, all the F_1 offspring, both males and females, will have red eyes and gray bodies. The genes for these characters are known to be located on the X-chromosome, so that the ordinary expectation of F_2 can be easily ascertained by referring to Figure 6.17. If one of these heterozygous females with red eyes and gray bodies is then mated to a male with white eyes and a yellow body, 99 per cent of the offspring are of the expected kinds: equal numbers of males and females with red eyes and gray bodies and with white eyes and yellow bodies (Fig. 6.24). The other 1 per cent is made up of equal numbers of males and females with red eyes and yellow bodies and with white eyes and gray bodies. These individuals arise from zygotes containing chromosomes in which crossing over has occurred. Crossing over has been extensively studied, and the percentage of cross-over types to be expected in given crosses is known; the amount of crossing over differs among different genes. The concept that genes are arranged in a given linear order was deduced from crossing over, and chromosome maps showing the distances between the loci occupied by certain genes have been compiled from the data collected on crossing over (Fig. 6.16).

The changes in combinations of entire linkage groups that occur from generation to generation as a result of disjunction of homologous chromosomes and subsequent combinations of gametes, as well as the changes in gene



Two pairs of homologous chromosomes showing positions of allelomorphic genes.

Crossing over: The chromosomes of the pair shown in A may twist about one another as in C and break in the plane of the dotted line so that comparable sections are exchanged as shown in D.

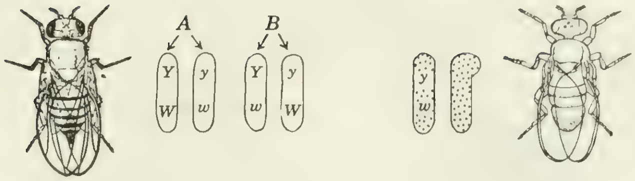
Deletion: One member of the chromosome pair shown in A may twist on itself as in E and break in the plane of the dotted line so that an internal section containing gene *c* is lost, or deleted, as shown in F.

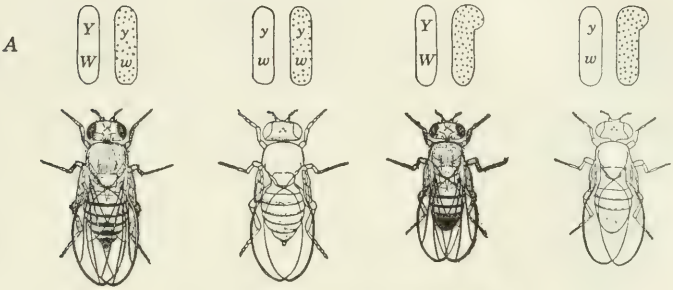
Inversion: One member of the chromosome pair shown in A may twist on itself as in G and break in the plane of the dotted line so that the section containing genes *B* and *C* is inverted as shown in H.

Duplication and deficiency: If one member of the chromosome pair shown in A comes to lie across the other as shown in I and a break occurs in the plane of the dotted line, the chromosome on the left in J will have a duplication and contain both gene *d* and gene *D*, and the chromosome on the right will have a deficiency of the section containing gene *D*.

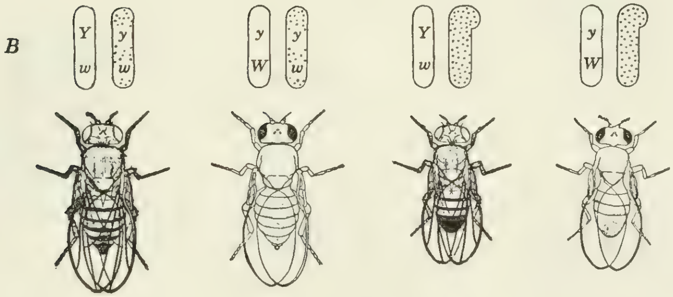
Translocation: One member of the chromosome pair shown in A may come to lie across one member of the chromosome pair shown in B, as seen in K. If a break occurs in the plane of the dotted line, sections of non-homologous chromosomes are exchanged, or translocated, as shown in L.

Fig. 6.23. Crossing over and various chromosomal aberrations; diagrammatic.





Non-cross-over progeny 99%



Cross-over progeny 1%

Fig. 6.24. The effect of crossing over in a case of sex-linked inheritance. A heterozygous female *Drosophila* with red eyes and gray body is mated with a male which has white eyes and a yellow body like her father. Ninety-nine per cent of the offspring (shown at *A*′) are of the expected or non-cross-over types that result when the X-chromosomes at *A* pass into ova and combine with sperm. One per cent of the offspring (shown at *B*′) have unexpected combinations of eye and body colors; these develop from zygotes that have received chromosomes in which crossing over has occurred (shown at *B*). Chromosomes from the female are represented as empty, and those from the male are dotted. *Y* and *y* are the genes for gray and yellow body color; *W* and *w* for red and white eye color (cf. Fig. 6.23 *C* and *D*).

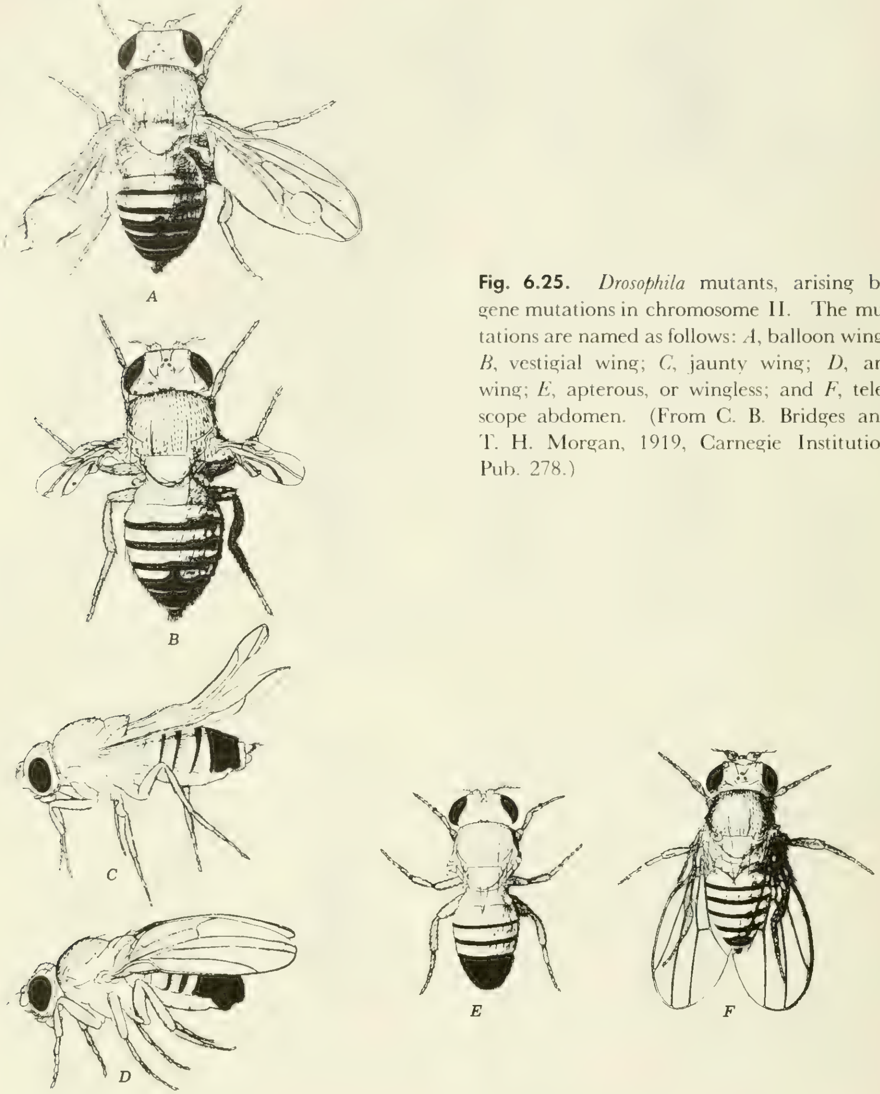


Fig. 6.25. *Drosophila* mutants, arising by gene mutations in chromosome II. The mutations are named as follows: *A*, balloon wing; *B*, vestigial wing; *C*, jaunty wing; *D*, arc wing; *E*, apterous, or wingless; and *F*, telescope abdomen. (From C. B. Bridges and T. H. Morgan, 1919, Carnegie Institution Pub. 278.)

associations within linkage groups that arise from crossing over, are merely shifting of genes without change of their quality or quantity; that is, the genes are present in the expected numbers and unaltered in kind. When the complete results of breeding are examined, however, we find that there are changes in single genes and in groups of genes which produce noticeable changes in the characteristics of an individual and which are heritable. Heritable variations are the only source of new kinds of organisms, the material of organic evolution (pp. 636 and 648). Such variations fall into two classes: those arising by an alteration, or mutation, of a particular gene, and those resulting from what are known as chromosomal aberrations which give rise to changes in the numbers of genes or in their relationships to one another in the linkage groups.

Gene mutations are ordinarily thought of as changes in the quality of a given part of the gene string. Hundreds of such mutations have been discovered in the many thousands of *Drosophila* that have been examined, although the number of times that any particular mutation has occurred is very small (Fig. 6.25). One gene has been recorded as mutating 4 times in the formation of 500 gametes, another 2 times in 1800 gametes. When all the genes in chromosome II of *Drosophila* were considered, it was found that only 30 mutations occurred in 5000 chances. Not all genes mutate with the same frequency, and very few, apparently, change often under normal conditions. Mutations produce changes in the structure of organisms and in the way they function. Many mutations that tend to alter function result in the death of the organism; they are called lethal mutations.

Chromosomal aberrations involve parts of chromosomes, whole chromosomes, and even entire haploid sets of chromosomes. The fact that losses or additions of genes in the cell produce observable changes in the individual reminds us that genes ordinarily interact with one another in what must be thought of as a balanced condition. If this balance is shifted by adding or subtracting groups of genes, the effect may be to kill the individual; with other aberrations the individual may live but be unable to produce functional germ cells. Sometimes such aberrations can be handed on from one generation to the next. The various types of alterations in linkage groups can be described briefly.

Alteration in a linkage group may be brought about by loss of a certain region of a chromosome. This is known as **deletion**, and an individual in which a deletion occurs will contain only one of each of the genes located in that region of the chromosome (Figs. 6.20 and 6.23*E* and *F*). Sometimes breeding results indicate that **inversion** has taken place; that is, a portion of the gene string has been reversed in postion (Fig. 6.23*G* and *H*). It is of considerable interest that alteration of the linear order may produce a heritable effect different from that resulting from the same genes in their typical sequence. Occasionally, a part of one chromosome becomes attached to the other member of a pair in such a way that one chromosome has a given region duplicated, whereas its homologue is **deficient** for the same region and the genes it carries (Fig. 6.23*I* and *J*). This is, in effect, an unequal crossing over. Another type of shift in linkage relations occurs when pieces of nonhomologous chromosomes become interchanged (Fig. 6.23*K* and *L*). This is known as **translocation**. What cytological evidence there is concerning the chromosomal behavior responsible for these altered linkage relationships indicates that, when the chromosomes are in the form of long threads during the early growth period, they may come into contact with one another, stick together, and sometimes be broken when the contractions of the threads occur.

It has been established by careful studies on the fruit fly, maize, and cotton that linear clusters of hereditary units known as **pseudo-alleles** occur. These have distinct but related functions. They are assumed to have arisen by duplication and reduplication of an original limited region of the chromosome, an assumption which rests on both cytological and genetical evidence. The repeated units may undergo mutation in different ways, thus making possible evolution of the functional units of heredity.

An entirely different type of abnormal chromosomal behavior sometimes occurs during the meiotic divisions. Homologous chromosomes may fail to separate from one another and, therefore, will pass together into one cell. This is known as **non-disjunction** and can involve any pair of chromosomes. One resulting cell will lack a whole chromosome of the typical haploid set, whereas the other will have a haploid set plus one chromosome. Fertilization will result in some individuals which have only one chromosome of a particular pair and in others which have three such chromosomes. These individuals will lack one complete gene string or have an extra one. In *Drosophila* non-disjunction of X-chromosomes and of the smallest chromosomes (IV) is known to occur (Fig. 6.26). Non-disjunction of the X-chromosome gives rise to females and males with unexpected characteristics, since some females get both X-chromosomes from their mother and some males get an X-chromosome from their father. Non-disjunction of chromosome pair IV produces haplo-IV and triplo-IV individuals differing from one another and from the normal diplo-IV fly in appearance. Entire sets of chromosomes may fail to disjoin, so that a gamete will contain the diploid rather than the usual haploid number of chromosomes. If fertilization adds a haploid set to such a diploid gamete, the zygote has three chromosomes of each kind and gives rise to a **triploid** individual. In *Drosophila* such flies are conspicuously different from the diploid or normal type.

Individuals that have four or more chromosomes of each set are also known. They may arise as a result of an incomplete mitosis at the time of the first cleavage of the zygote. The chromosomes undergo reduplication but do not separate, so that the number is doubled and a **tetraploid** individual develops. Such organisms usually are conspicuously larger than their diploid relatives. Chromosome doubling sometimes occurs when gametes from two different species of plants have united. Subsequent synapsis between pairs of homologous chromosomes is thus made possible, and functional gametes may be formed. This usually does not occur in hybrids between different species, such as the mule. Several entirely new species of plants are known to have been established by chromosome doubling in a hybrid, but so far no comparable cases have been discovered among animals.

Since gene mutations and chromosomal aberrations offer very interesting material for the study of the mechanism of heredity, many investigators have attempted to increase the rate at which such alterations occur. *Drosophila* was subjected to high and low temperatures, various nutritional modifications, and treatment with a great many chemicals, but with no appreciable change in the frequency of the appearance of mutations. It remained for H. J. Muller to show in 1925 1926 that X rays greatly increased the number of chromosomal aberrations, as well as gene mutations. Other kinds of radiation as, for example, radium emanations and ultraviolet light have been shown to increase the rate of mutation. Some chemical compounds, such as mustard gas, have been proved mutagenic.

The manner of action of ionizing radiations, such as X rays, has been a baffling problem. Evidence increasingly supports the concept of an indirect effect rather than that of a direct hit by a particle on a gene target. Radiation of a living cell produces its primary effect on the solvent water, disrupting its molecules into H atoms and OH radicals; the H atoms may combine with O_2 to form HO_2 radicals. These free radicals, OH and HO_2, are very active chemically and involve the compounds of the cell in unusual reactions. Something which is produced as a consequence of these atypical reactions acts as a chemical mutagen to modify the genetic material in some way. The particular composition of the cell contents influences the response to radiations. Thus radiations appear to produce their effects by indirectly distorting the normal metabolic sequences of the cell. In germ cells the genonemata become modified in such a way as to affect the heredity of future generations.

It has been determined that the effects of ionizing radiations in producing mutations are directly proportional to the dose. This is true whether a given

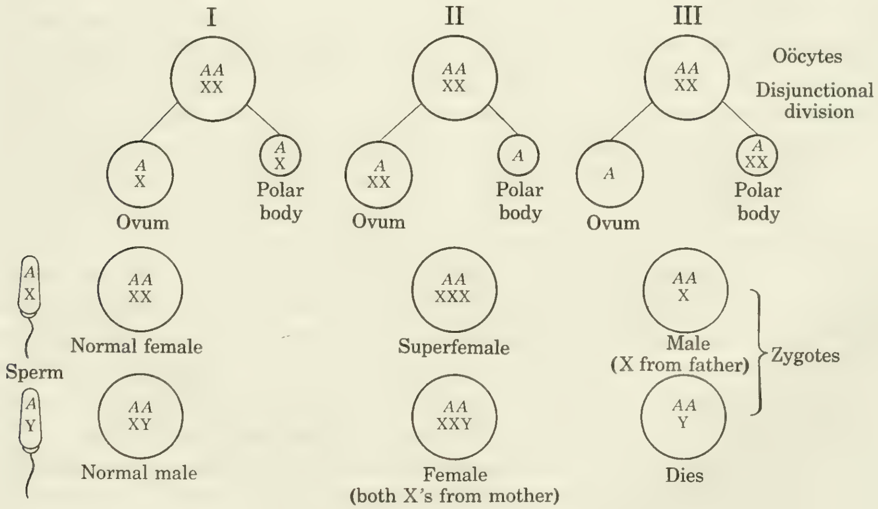


Fig. 6.26. Diagram showing, in column I, normal disjunction of the X-chromosomes in oögenesis and the subsequent possibilities of fertilization with typical sperm; in column II, non-disjunction of X-chromosomes, both remaining in the ovum, and subsequent fertilization; and in column III, non-disjunction of X-chromosomes, both passing to the polar body, and subsequent fertilization. *A* is used as a symbol for a complete haploid set of autosomes.

dose is received in a short time or distributed over a long period, whether continuous or intermittent. That is, the biological effects of ionizing radiations are cumulative. These facts, known for a long time, have assumed great importance for man in recent years. The use of X rays in diagnosis and treatment by the medical and dental professions has increased. Now, with experimental detonation of thermonuclear weapons there is unpredictable increase in radioactive fallout in the atmosphere. Radioactive waste from atomic power plants the world over may become an increasing source of contamination of water and air. Grave concern is felt, nationally and internationally, over the adverse genetic effects on man, as well as on his domesticated plants and animals. Of the mutations that have been induced in experimental animals and plants, the great majority have been detrimental, many producing death. It is evident that serious attention must be given to the necessity of keeping the total amount of radiation received by every individual below the critical level for genetic damage. The future of the human race is at stake.

Sex Determination

Animals are typically **dioecious**; that is, there are two sexes, which differ essentially in that the males produce microgametes, or spermatozoa, whereas the females produce macrogametes, or ova. In association with this primary distinction between males and females, we have seen that differences exist between the reproductive systems (p. 128). In many animals what are known as secondary sex characters are very conspicuous distinguishing features of the sexes. For example, the gay plumage of many male birds, the vocal differences between the sexes in many vertebrates from frog to man, and in some mammals the greater growth of hair in the males, as in the lion and man, differentiate the sexes. It is true that in numerous species of vertebrates, especially among lower animals, no such secondary sex characters can be observed, although there may be a size difference between the sexes.

Not all animals are sexually distinct; some are **monoecious**, or **hermaphroditic**, and every individual produces both microgametes and macrogametes. Sometimes hermaphroditic animals produce first sperm and later eggs, or vice versa, but frequently eggs and sperm are matured at the same time. Almost all plants are monoecious. We see that sexual differentiation between individuals is not by any means a universal attribute of living things. The production of differentiated gametes correlated with the capacity of reproduction is not dependent on the sexual differentiation of individuals.

The conspicuous differences between the sexes in the higher animals have long excited the curiosity of biologists and led to attempted explanations and hopes for control. Early hypotheses were formulated in terms of the nutritive conditions under which the young developed, in spite of the obvious fact that a litter of pups or kittens, for example, contains both males and females whose development has occurred under identical conditions. In man two kinds of twins are known. Fraternal twins may be of the same or opposite sex and bear no more resemblance to one another than other brothers and sisters, but identical twins are always of the same sex. A comparable situation is known in the nine-banded armadillo, which gives birth to four young, all of the same sex, and in certain insects, which produce by the method of polyembryony large numbers of young, all of the same sex. These situations were clarified by study which revealed that identical twins in man and other mammals and the quadruplets of the armadillo, as well as the polyembryos of insects developed from single zygotes, had identical hereditary constitutions.

Furthermore, the discovery and study of the so-called sex chromosomes led to the interpretation proposed by E. B. Wilson in 1905 that sex was determined at the time of fertilization by the chance combinations of the gametes formed. In the insect, *Protenor*, there are 14 chromosomes in the female but only 13 in the male (see Fig. 2.12*A*, *B*, and *C*, p. 42); and 7 pairs of chromosomes in the female, but only 6 pairs and an extra or odd chromosome in the male. The extra chromosome of the male can be clearly seen to be similar to one of the pairs of the female, the largest pair in this instance. This unpaired chromosome of the male and the comparable pair of the female are called X-chromosomes or **sex chromosomes**. All the other chromosomes, which occur in pairs in both males and females, are known as **autosomes**. If a haploid set of autosomes is designated as A, then a formula for the chromosome number of any somatic cell or primordial germ cell of a female *Protenor* would be $2A + 2X$, where X stands for a sex chromosome, and the formula for every mature ovum would be $A + X$. The chromosome content of somatic cells and undifferentiated germ cells of a male *Protenor* would be $2A + X$. One-half of the spermatozoa could be represented by $A + X$ and the other half by $A + O$. Wilson pointed out that, when an ovum $(A + X)$ was fertilized by one kind of spermatozoon $(A + X)$, the zygote would have the number of chromosomes characteristic of the female $(2A + 2X)$. If the ovum $(A + X)$ was fertilized by the other kind of spermatozoon $(A + O)$, then the zygote would have the number of chromosomes characteristic of the male $(2A + X)$. Since by the process of mitosis during development each cell receives the same number of chromosomes that the zygote has, it can be seen how the concept arose that sex was determined by the number of X-chromosomes present in the zygote.

It was soon discovered that the male did not always differ from the female in number of chromosomes and that, although the male had only one X-chromosome, it sometimes had a Y-chromosome that segregated from the X-chromosome at the disjunctional division (see Fig. 5.7, p. 135). The Y-chromosome, like the X, is known as a sex chromosome. *Drosophila* males have such a Y-chromosome (see Fig. 2.12*E*, p. 42) and produce two classes of spermatozoa, which can be represented as $A + X$ and $A + Y$. Union with $A + X$ ova yields female-producing zygotes $(2A + 2X)$ and male-producing zygotes $(2A + XY)$. In *Protenor*, which is an example of forms with XO

males, and *Drosophila*, which is an example of forms with *XY* males, the males are the **digametic sex**, or the sex that gives rise to two kinds of gametes with respect to the X-chromosome.

The diagrammatic simplicity of such a method of sex determination became somewhat confused when the observation was made that in some species of moths and in birds the female was the digametic sex; that is, a female moth produces two kinds of ova, one with an X-chromosome and one without, whereas all the spermatozoa are alike in carrying an X-chromosome. Many facts indicate an undeniably close correlation between number of X-chromosomes and sex, however. One of the most interesting is the occurrence of bilateral **gynanders**, which are male on one side and female on the other. It is clearly established that gynanders in *Drosophila*, for example, arise from female-producing zygotes ($2A + 2X$). At the time of the first division one of the X-chromosomes, either the paternal or the maternal, is lost on the mitotic spindle, so that one nucleus has $2A + 2X$ chromosomes and the other has $2A + X$ chromosomes. The former gives rise to the female half, the latter to the male half of the gynander. If the X-chromosome is lost in some later division, only a limited region of the female will exhibit male characteristics.

In spite of such confirmation of the sex-chromosome theory of sex determination, it should be obvious that the study of inheritance has shown characters to depend on combinations of the genes located in the chromosomes, not on the chromosomes as such. Yet with sex, the presence of two particular chromosomes was assumed to condition the differentiation of one sex, and one of these chromosomes was assumed to condition the differentiation of the other sex. Either one of the X-chromosomes of a female could enter a male-producing zygote, and the X-chromosome of a male could pass into a female-producing zygote. No gene for maleness or femaleness has been located on the chromosome maps of *Drosophila* or with certainty been identified in any species, although reported by some investigators. The discovery of intersexes among the offspring of triploid females by C. B. Bridges in 1921 led to his formulation of the **Theory of Genic Balance** to explain the determination of sex. When disjunction occurs in the germ cells of triploid ($3A + 3X$) females, some eggs with $2A + X$ chromosomes and some with $A + 2X$ are formed, among others. If a $2A + X$ ovum is fertilized by an $A + X$ sperm, a $3A + 2X$ zygote results and develops into an **intersex**, or an individual that is male in some parts and female in others. These male and female parts are not clearly segregated into halves or quarters as in gynanders but are completely blended, and intersexes range from almost total females to almost total males. Bridges' theory is that sex is the result of the interaction of many different genes, some of which are to be thought of as female determiners and others as male determiners. Both types of genes are located on all the chromosomes. However, there are more female than male determiners in the X-chromosomes, whereas the reverse situation is true in the autosomes. The distribution and effect of these genes are such that, when a zygote has a $2A + 2X$ constitution, the female determiners on the X-chromosomes overbalance the male determiners on the autosomes. When the zygote has a $2A + XO$ or $2A + XY$ constitution, the male determiners on the autosomes overbalance the female determiners on a single X-chromosome; the Y-chromosome appears to carry no genes related to sex. In the $3A + 2X$ individuals neither set of genes overbalances the other, but both are somewhat effective in molding the appearance of the intersex. This theory is strengthened by the occurrence of what are known as superfemales and supermales in which the chromosomal make-up is $2A + 3X$ [ovum $(A + 2X)$ + spermatozoon $(A + X)$] and $3A + XY$ [ovum $(2A + X)$ + spermatozoon $(A + Y)$], respectively. Although triploid $(3A + 3X)$ and tetraploid $(4A + 4X)$ individuals are females, as would be expected on the basis of an explanation in terms of genic balance, haploid individuals $(A + X)$ are males in bees and other forms that normally produce males parthenogenetically. Haploid drosophilas have not been found, so that the theory remains untested in a crucial case. More facts are necessary before the final word can be said on the mechanism of sex determination at fertilization. We have seen an apparently satisfactory theory in terms of $2X$ versus XO or XY zygotes fail to explain accumulated observed facts and hence undergo modification. Such is the method of science—observation, explanation, further observation or experimentation, and modification of explanation when necessary—a continued seeking for the whole truth.

As in all development, the environment influences the differentiation of so-called sex characters. A zygote in which the genic balance is female-determining may develop into a male in an atypical environment. In 1915 Emil Witschi found that if frogs were forced to develop at a high temperature, they were all males because the female-producing genotype had been overridden by environmental conditions. Sometimes reversal of sex occurs. A hen, for example, may change into a cock and produce spermatozoa. Although the mechanism of the overriding of the inherited constitution, the genotype, is not clear, this is only a special case of the effect of the environment, as noted previously (pp. 167 and 195).

The problem of sex determination is not really a special one, although it has long been so treated. It is well known by geneticists that single pairs of genes do not by themselves produce an effect in the organism. They always depend on the presence of other genes, on a given pattern of distribution of the cytoplasm of the zygote during cleavage and the cell movements during development, on interactions between differentiating cells, and on the chemical and physical conditions of the external environment. In the ordinary course of events the genes are the part of this complex most often varied; that is, new combinations of genes occur with each fertilization, but development proceeds under practically uniform conditions in the great majority of cases. Genes initiate chains of reactions which may be environmentally modified during cell differentiation. When the environment is altered, its importance in the complex of factors determining what the individual will be, not only with respect to its sex but also its other characteristics, is appreciated.

Summary

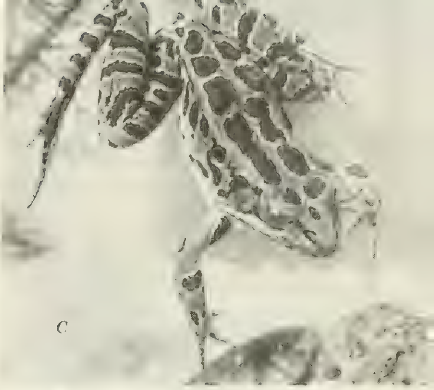
The genes located in the chromosomes of the nucleus have been found to be responsible for all types of similarities between individuals related by descent, from gross morphological characteristics to single enzyme-directed metabolic reactions. In fact, insofar as we know, everything that a living cell does can be referred in the final analysis to genic initiation and direction. If these amazing self-perpetuating units were immutable, it may be supposed that all living organisms would be identical within narrow limits, reflecting environmental influence on genic expression. A great common pool of genes is obviously present in living organisms as evidenced by the many similarities that exist in the reactions of all cells. But innumerable changes have occurred through the ages that living things have existed on the earth. You will become acquainted with the great diversity of animal life as you continue your study of zoology. The capacity of genes to become changed and to perpetuate that change has provided the material from which the environment has selected during the process of organic evolution. Not only is the past and present status of living organisms conditioned by the genes they carry, but their future potentialities are latent in the possibilities for change in the genome. Is it any wonder that many scientists work with all the resources at their command to determine the nature of the gene?

CHAPTER 7

CHAPTER 7

THE CLASSIFICATION

The preceding chapters have presented an introduction to zoology through the study of structure and function in vertebrate animals. This introduction has illustrated the organization of vertebrates and their capacities of metabolism, responsiveness, and reproduction, as well as the nature of development and heredity. From the standpoint of function such an introduction would suffice for animals in general; the characteristics and activities of the cells are essentially alike in the bodies of all animals. It may be said that all living things are faced with common problems of survival, and the functional solutions of these problems are similar in many diverse types of animals. From the standpoint of structure, however, study of the vertebrates alone is inadequate. There are many kinds of animals very different from vertebrates in their organization, although their general functions may be very similar. In the chapters to follow some of these different types of animals will be examined, particularly as they illustrate principles of **morphology, ecology,** and **evolution.** As an introduction to this survey, we may consider briefly the diversity of animal life and some of the evidence indicating that all the diverse types will fit into an orderly system, based on structural similarities and believed to indicate evolutionary relationships. Let us begin by examining the principles, methods, and implications of the classification of animals.



OF ANIMALS

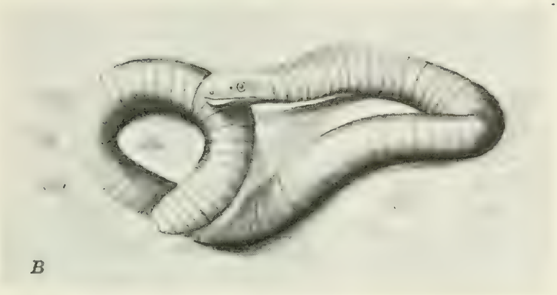


Fig. 7.1. The orders of the class Amphibia. *A*, order Caudata: the mud puppy, *Necturus maculosus*. *B*, order Apoda: a caecilian, or limbless amphibian, *Siphonops annulatus*. *C*, order Salientia: the pickerel frog, *Rana palustris*. (*A* and *C*, photographs courtesy New York Zoological Society; *B*, redrawn, after Claus-Grobben, from W. Stempell, 1926, *Zoologie im Grundriss*.)

Classification

Historical. Confronted with any large array of diverse facts or forms, man finds it necessary to catalog or classify them before they are understandable in relation to each other. This need to classify, to group like with like, has been felt since earliest times in studies of the vast numbers of living things inhabiting the earth. The first serious attempt to classify animals logically and scientifically, on the basis of similarities and differences in fundamental characteristics, was made by Aristotle (384–322 B.C.). During later centuries other systems of classification were erected, and comparisons were drawn between the structures of animals and those of plants. These early systems were not widely accepted, and the classification that developed into the modern scheme was not formulated until the eighteenth century. Almost all the early systems suffered from the fact that relatively little was known of the fundamental characteristics of living things; these systems were based largely on superficial or artificial criteria.

In general, the classification of plants progressed more rapidly than that of animals. John Ray (1628–1705) attempted to classify both animals and plants in a single system, emphasizing structure as the basis of comparison.

SUBKINGDOM PROTOZOA
PHYLUM PROTOZOA

- Subphylum Plasmodroma
  - Class Sarcodina
  - Class Flagellata
  - Class Sporozoa

- Subphylum Ciliophora
  - Class Ciliata
  - Class Suctoria

SUBKINGDOM METAZOA

PHYLUM MESOZOA

PHYLUM PORIFERA

PHYLUM COELENTERATA
  - Class Hydrozoa
  - Class Scyphomedusae
  - Class Anthozoa

PHYLUM CTENOPHORA

PHYLUM PLATYHELMINTHES
  - Class Turbellaria
  - Class Trematoda
  - Class Cestoda

PHYLUM NEMERTINEA

PHYLUM ASCHELMINTHES
  - Class Rotifera
  - Class Nematoda
  - Class Gastrotricha
  - (Other minor classes)

PHYLUM ACANTHOCEPHALA

PHYLUM ENTOPROCTA

PHYLUM ECTOPROCTA

PHYLUM PHORONIDEA

PHYLUM SIPUNCULOIDEA

PHYLUM ECHIUROIDEA

PHYLUM MOLLUSCA
  - Class Amphineura
  - Class Pelecypoda
  - Class Gastropoda
  - Class Scaphopoda
  - Class Cephalopoda

PHYLUM ANNELIDA
  - Class Archiannelida
  - Class Polychaeta
  - Class Oligochaeta
  - Class Hirudinea

PHYLUM ONYCHOPHORA

PHYLUM ARTHROPODA
- Subphylum Trilobitomorpha (Ext.)
- Subphylum Chelicerata
  - Class Xiphosurida
  - Class Eurypterida (Ext.)
  - Class Pycnogonida
  - Class Arachnida
- Subphylum Mandibulata
  - Class Crustacea
  - Class Diplopoda
  - Class Chilopoda
  - Class Insecta
  - (Other minor classes)

PHYLUM CHAETOGNATHA

PHYLUM BRACHIOPODA

PHYLUM ECHINODERMATA
- Subphylum Pelmatozoa
  - Class Cystoidea (Ext.)
  - Class Blastoidea (Ext.)
  - Class Crinoidea
- Subphylum Eleutherozoa
  - Class Asteroidea
  - Class Ophiuroidea
  - Class Echinoidea
  - Class Holothuroidea

PHYLUM HEMICHORDATA

PHYLUM CHORDATA
- Division Acraniata
  - Subphylum Urochordata
  - Subphylum Cephalochordata
- Division Craniata
  - Subphylum Vertebrata
    - Superclass Pisces
      - Class Agnatha
      - Class Placodermi (Ext.)
      - Class Chondrichthyes
      - Class Osteichthyes
    - Superclass Tetrapoda
      - Class Amphibia
      - Class Reptilia
      - Class Aves
      - Class Mammalia

Fig. 7.2. The phyla of the Animal Kingdom and their principal subdivisions.

Ray adopted the concept of the **species**, limiting the term to forms producing offspring like themselves when bred together; this definition has much in common with the modern understanding of this important concept. However, it remained for Linnaeus (1707-1778), justly called the Father of Classification, to establish the basic structure of the present-day system. Linnaeus was by training more of a botanist than a zoologist, although he zealously studied animals as well as plants and developed a classification that included most of the animals known to him. His work with animals was less successful than his botanical work; nevertheless, the fact that he was able to formulate a scheme which became widely accepted, and which served as the basis for the modern system, justifies his enduring fame in the field of biological science called **taxonomy** (Greek, "law of arrangement"). Linnaeus' most significant contributions to classification were (1) his use of **structure** as the basis of comparison between forms, and (2) his establishment of **binomial nomenclature**, by which each organism is given a **generic** and a **specific** name.

The Modern System. It is a familiar fact that animals fall into restricted groups called **species** (singular species, not specie), which may be approximately defined as groups whose members successfully interbreed and resemble each other more than they resemble the members of other similar groups. The individuals, which are the ultimate material of classification, can thus be grouped into species. Different species with much in common form genera, similar genera form families, similar families form orders, and so on. We may begin with the individuals and species, as did early investigators; or, as the system is now established, we may begin with a larger group and follow its subdivisions until the species and individuals are reached. For example, the existence of a large group of animals known as **Vertebrata** was recognized after it had been discovered that a great array of animals possessed backbones composed of vertebrae. Later, it was found that several types of animals without vertebrae, and with relatively simple organization, possessed certain features in common with the vertebrates, particularly a **notochord** such as occurs in the early embryos of all vertebrates. The Vertebrata were then placed, along with these simpler groups, within a single **phylum**, one of the principal subdivisions of the Animal Kingdom. Despite the fact that this phylum, the **Chordata**, includes a very wide range of animal types, all chordates have certain basic features in common. These common, distinguishing characteristics include the presence, in the adult or at some stage of development, of (1) a primitive axial skeleton, the notochord, (2) gill slits, or traces of these structures, and (3) a dorsal, tubular central nervous system.

The principal subdivisions of the phylum Chordata are listed in Figure 7.2. One of these subdivisions is the subphylum **Vertebrata**, including, among others, the class **Amphibia**. Within this class, the existing forms may be classified as follows:

Class **Amphibia** (Fig. 7.1)
  Order **Caudata**, salamanders, newts, etc.
  Order **Apoda**, limbless, worm-like amphibians
  Order **Salientia**, frogs and toads.

After the **orders**, proceeding to smaller groups, come **families**, then **genera** (singular genus), and finally **species**. Thus, the order **Salientia** contains, along with some half dozen other families, the family **Ranidae**, which in turn includes the genus *Rana* and other genera. The genus *Rana* consists of several closely related species. The relationships of these categories may be shown as follows:

Order **Salientia.**
  Family **Ranidae.**
    Genus *Rana.*
      Species *Rana pipiens* Schreber, the leopard frog.

It will be noted that, in referring to the species, it is proper to use both generic and specific names; that is, the name of the animal commonly called the leopard frog is *Rana pipiens* or *R. pipiens*, not *pipiens* alone. The generic name is always capitalized, the specific name always written with a small letter. In the complete form, the name of the species is followed by the name of the individual who originally described it, and the date of the description is given in parentheses. Several of the species making up the genus *Rana* are *R. catesbeiana*, the bullfrog; *R. clamitans*, the green frog; *R. sylvatica*, the wood frog; *R. palustris*, the pickerel frog; and *R. pipiens*, the leopard frog.

A species containing groups of animals with relatively slight but constant differences is often divided into subspecies or varieties. The amount of difference between the individuals composing any one species can be appreciated only by examining a large number of specimens and making comparisons. In general, the differences that separate subspecies or varieties within species are less than those separating species. Whether a group shall be called a variety of an existing species, described as a new species, or made the basis of a new genus depends on the judgment of the individual making the classification.

The system of cataloging animals just described illustrates the principles of classification followed at the present time. Beginning with a group of animals, such as a species of frog or grasshopper, we can follow its classification into larger and larger groupings until the phylum is reached, and finally the **Animal Kingdom,** which is coordinate with the other great group of living things, the **Plant Kingdom.** Conversely, if we began with the Animal Kingdom, we might follow its branches into every subdivision until all the species were reached, and pass in review the diversified known forms of animal life. The modern taxonomic system is the result of years of study, in which hundreds of thousands of species have been described and arranged in accordance with their similarities to other forms. Such a system is necessary as a means of cataloging the multitudinous organisms constituting the Animal Kingdom.

But classification, as it is now undertaken by biologists, is more than a cataloging system. The basis of classification is structure, and it can be confidently assumed that structural similarities are indicative of ancestral relationships. Since the acceptance of the Theory of Organic Evolution, which followed the publication of Charles Darwin's *Origin of Species* in 1859, classification has become a never-ending effort to express evolutionary relationships between animals, as well as to furnish a catalog of types. For this purpose the functions of the parts of an organism are not important, for even in animals of the same phylum comparable parts often have entirely different functions. The basic structure of the parts is significant because this structure is found to be the same despite modifications correlated with different uses in different animals. The fore limbs of various vertebrate animals furnish examples of modifications of comparable parts in adaptation to diverse functions. The wings of birds and of bats, the fore limbs of horses, dogs, mice, frogs, monkeys, and so on, have all been modified in various directions in adaptation to various uses; but the underlying structural basis of the fore

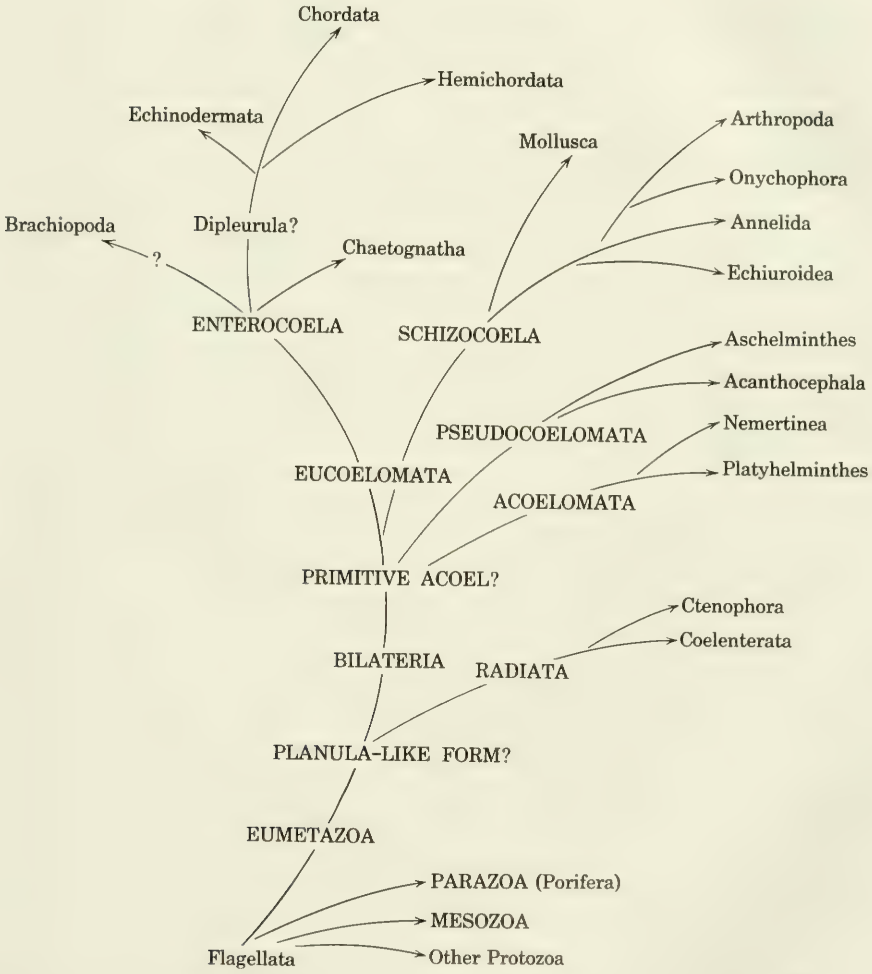

Chordata
Hemichordata
Echinodermata
Mollusca
Arthropoda
Onychophora
Brachiopoda
?
Dipleurula?
Chaetognatha
Annelida
Echiuroidea
ENTEROCOELA
SCHIZOCOELA
Aschelminthes
Acanthocephala
PSEUDOCOELOMATA
Nemertinea
Platyhelminthes
EUCOELOMATA
ACOELOMATA
PRIMITIVE ACOEL?
Ctenophora
Coelenterata
BILATERIA
RADIATA
PLANULA-LIKE FORM?
EUMETAZOA
PARAZOA (Porifera)
MESOZOA
Flagellata
Other Protozoa

Fig. 7.3. A phylogenetic tree of the Animal Kingdom, designed to show the possible interrelationships of the various phyla. Such a figure should be interpreted as a statement of evolutionary probabilities and not as a precise representation of the exact course of evolutionary change.

limb is similar in all. Structures in different animals which reveal, like the fore limbs of vertebrates, basic similarities in organization and in embryonic origin, are spoken of as **homologous** structures. In contrast, parts of animals which are of diverse origin and composition, even though they may be adapted to similar functions, are said to be **analogous**; the wings of birds and the wings of insects are examples often cited. In classifying animals, then, we depend not on the functional similarities of analogous parts but on the more fundamental and significant structural similarities exhibited in homologous features.

At the present time, many species of animals remain to be cataloged, and the taxonomic positions of known species are undergoing constant revision as additional information and insight seem to warrant. Therefore the "family tree" of living things cannot be drawn with certainty in all its features, although many lesser conclusions can be drawn with reasonable accuracy, considering the nature of the evidence. Upon this tentative basis the tree of descent shown in Figure 7.3 is presented; but before considering in detail what this figure means, we should examine the catalog of animal types now known to us.

The Principal Types of Animals. In accordance with the foregoing principles of classification, by which animals are arranged in species, genera, families, and so on, zoologists have arrived at the present comprehensive system. Sweeping changes have been made, in the past, as knowledge of new types or new facts about known types have accumulated. It appears, however, that classification of the major phyla and their main subdivisions now rests upon a fairly permanent basis.

During the earlier years of this century there was wide acceptance, at least by American zoologists, of a system including 12 or 15 animal phyla, to which lesser groups of questionable status and affinities were appended. More recently, the tendency has been toward an increasing number of phyla, in recognition of the distinctive features of many of the smaller groups. There appears to be no serious objection to the elevation of a minor group to the rank of a phylum if its characteristics are sufficiently different from those of other animals to justify the change. Hyman, whose studies have done much to elucidate possible interrelationships between invertebrate groups,[1] makes the following statement: "A phylum should consist of closely allied animals distinguishable from any other phylum by well-defined positive characteristics, some of which do not exist in any other phylum or not in that particular combination. Any group of animals, however small, having such distinct characters, should be regarded as a separate phylum until evidence

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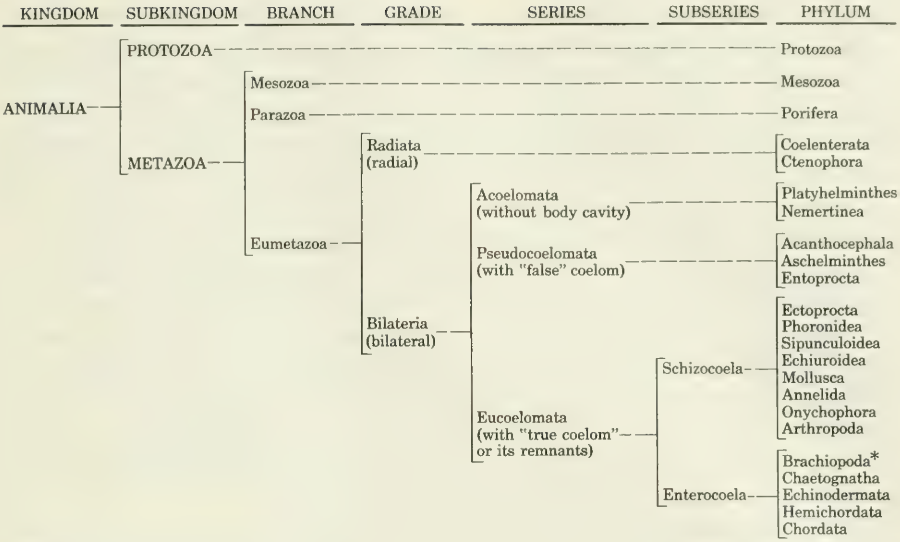
[1] The term invertebrate is used generally to include animals without vertebrae, or backbones. The distinction between vertebrates and invertebrates, although convenient, is artificial from the taxonomic standpoint. It cuts across the phylum Chordata, some members of which are vertebrates and some invertebrates. It thus appears in contrast to the distinction between the phyla, or between the Protozoa and the Metazoa.


KINGDOM
SUBKINGDOM
BRANCH
GRADE
SERIES
SUBSERIES
PHYLUM
ANIMALIA
PROTOZOA
Protozoa
METAZOA
Mesozoa
Mesozoa
Parazoa
Porifera
Eumetazoa
Radiata (radial)
Coelenterata
Ctenophora
Bilateria (bilateral)
Acoelomata (without body cavity)
Platyhelminthes
Nemertinea
Pseudocoelomata (with "false" coelom)
Acanthocephala
Aschelminthes
Entoprocta
Eucoelomata (with "true coelom" or its remnants)
Schizocoela
Ectoprocta
Phoronidea
Sipunculoidea
Echiuroidea
Mollusca
Annelida
Onychophora
Arthropoda
Enterocoela
Brachiopoda*
Chaetognatha
Echinodermata
Hemichordata
Chordata

*Some brachiopods are apparently schizocoelous in their mode of coelom formation, but this may be a secondarily derived characteristic.

Fig. 7.4. Interrelationships among the phyla of animals, based on similarities and differences in broad, general characteristics.

shall be forthcoming showing its relationship to some other phylum."[2] In the treatise from which this quotation was taken, Hyman lists 22 phyla; 23 are now commonly recognized (see Fig. 7.2), and an additional new phylum has recently been proposed to contain an aberrant group of animals, the **Pogonophora**, dredged from ooze on the deep ocean floor.

Some of these phyla are small in numbers of species, and many consist of animals not easily available and hence relatively unknown except to specialists. For the purposes of the present chapter, only the larger and better-known phyla need to be considered in any detail. It can then be remembered that the Animal Kingdom includes certain lesser groups, which may also be classified as phyla, although even today authorities differ on many details of classification. For example, the phylum Aschelminthes has been proposed to include several problematical groups classified in different combinations by various authorities; many zoologists do not interpret the evidence for the interrelationships of these forms as justifying their inclusion in a single phylum.

The list of phyla and their principal subdivisions in Figure 7.2 is inserted for reference and orientation; some minor groups have been omitted. As you proceed, the names of the larger phyla, such as Protozoa, Coelenterata, Arthropoda, and Chordata, as well as of some of their subdivisions, will become familiar.

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[2] Quoted by permission from L. H. Hyman, *The Invertebrates: Protozoa through Ctenophora,* copyright 1940 by McGraw-Hill Book Co., Inc., page 32.

As we have seen, an individual phylum is made up of related classes containing animals with similar fundamental characteristics. We assume that similarity in structure implies common ancestry, and therefore that members of the same phylum are more closely related to each other than to members of other phyla. It is significant also that the various phyla can be grouped into larger categories, on the basis of similarities and differences in large general characteristics, as shown in Figure 7.4. A study of this figure will demonstrate that just as a phylum can be subdivided into classes, orders, and lesser ranks, the Animal Kingdom can be subdivided into subkingdoms, branches, grades, series, and subseries. For purposes of grouping the phyla into these larger categories, use is made of more general and fundamental characteristics. These include the **grade of organization,** the **kind of symmetry,** and the **presence or absence, and kinds, of body cavities.** Since these features are of such a basic nature and make possible such sweeping and general distinctions within the Animal Kingdom, we may consider briefly what they involve in terms of the structure of animals.

► **Grade of organization.** This criterion distinguishes the kind of construction, whether unicellular as in the Protozoa, or multicellular, as in all other animals. Among the multicellular forms, the Mesozoa and Parazoa are said to represent the **cellular** grade of construction, with little or no differentiation into tissues. All the higher animals, on the other hand, constituting the Eumetazoa, possess groups of similar cells specialized for the performance of particular functions and so are said to exemplify the **tissue** grade of organization.

► **Kind of symmetry.** Among the Eumetazoa, two kinds of symmetry are distinguishable. One, characteristic of the Coelenterata and Ctenophora, is termed **radial** symmetry and is marked by the presence of a principal axis of the body, about which the parts are disposed in a radiating pattern. In contrast to this, all the more complex metazoans possess **bilateral** symmetry, in which there is one median or sagittal plane dividing the body into right and left halves which are approximately mirror images of each other. There are apparent correlations between forms of symmetry and ways of life in animals. Radial symmetry is primarily associated with sessile or attached animals, which are in approximately equivalent contact with their environment in all directions; in radially symmetrical animals there are commonly differentiations between oral and aboral ends, or between the free end and the attached end, so that an axis of polarity usually corresponds to the axis of symmetry. Bilateral symmetry, on the other hand, is generally associated with active, free-moving ways of life, and in addition to **right and left sides** and **head and tail ends, back and belly surfaces** may usually be distinguished.

► **Body cavities** (Fig. 7.5). Some of the bilateral animals have no cavities within the body other than that of the digestive system; these are termed **acoelomate.** Among the metazoans which do possess a body cavity surrounding the digestive tract, this cavity may have different characteristics and may arise in different ways. For example, the members of the series **Eucoelomata**

(Fig. 7.4) possess a body cavity termed a **coelom**, which is lined by a layer of mesodermal tissue, the peritoneum. The manner of origin or mode of formation of the coelom differs in consistent ways in different kinds of eucoelomate animals, and these facts are used in distinguishing between the two subseries which can be recognized. In contrast, members of the series **Pseudocoelomata** have a body cavity which is not a coelom but a **pseudocoel** with no peritoneal lining.

Considering these broad, general characteristics, the phyla may be grouped into larger subdivisions, according to a classification which seems reasonable to many zoologists. It should be pointed out that these larger categories, the branches, series, and so on, are not recognized taxonomic entities with the same standing as, for example, the species, the family, or the phylum. They are rather to be regarded as synthetic groupings, useful as aids to an understanding of the similarities and differences, **and thus the probable ancestral relationships,** between the members of the various phyla.

It should be realized also that any classification represents merely an opinion of experts, based on the knowledge available at a given time. Aristotle, for example, working in the fourth century B.C. with very little information other than that which he himself could accumulate, classified animals as those with red blood (essentially our vertebrates) and those without red blood (our invertebrates). Early in the nineteenth century, the great French naturalist Cuvier (1769–1832) divided the Animal Kingdom as it was known to him into four main types: **Vertebrata, Articulata, Mollusca,** and **Radiata (Zoophyta).** With increasing knowledge and increasing insight, it was later recognized that each of these groups included forms so diverse that they could not properly be classified together. Subsequent changes in Cuvier's scheme involved the separation of the Articulata into the joint-footed **Arthropoda** and the worm-

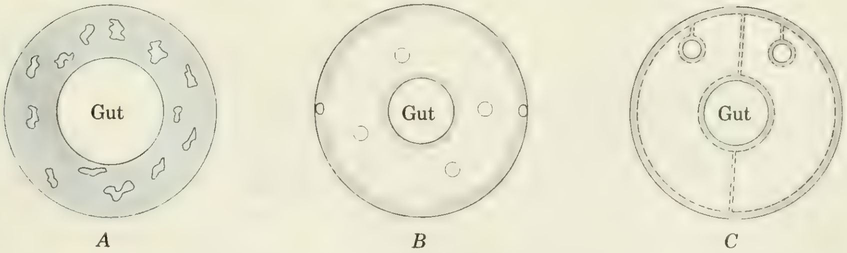
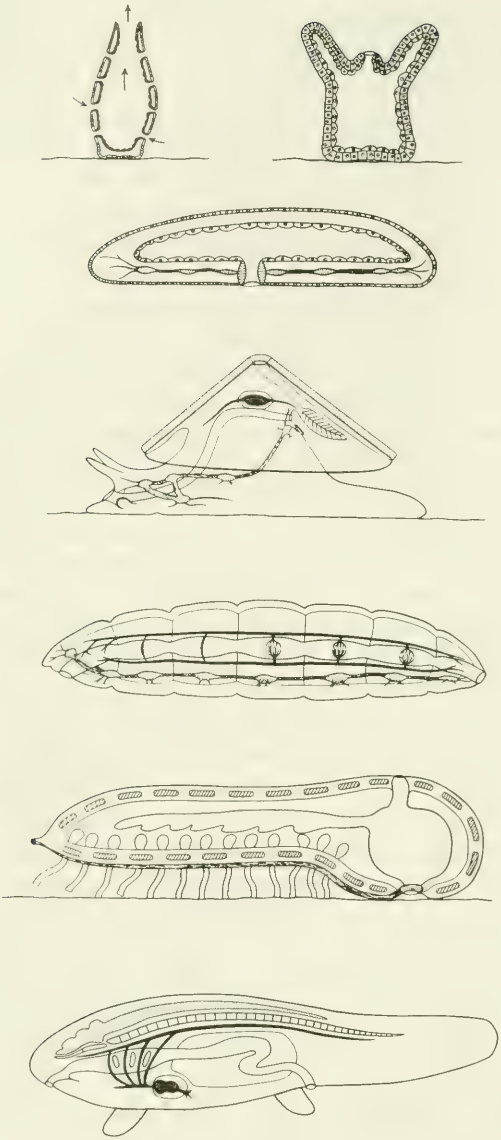


Fig. 7.5. Schematic cross sections for comparison of acoelomate, pseudocoelomate, and eucoelomate plans of organization. *A*, acoelomate: epidermis and gastrodermis are separated by mesenchymal "parenchyma," through which lymph-like fluid percolates. *B*, pseudocoelomate: the body wall encloses a cavity which contains muscular and other elements of mesodermal origin, but the cavity is not lined, or the structures covered, by a peritoneal layer. *C*, eucoelomate: the body cavity is a true coelom, lined throughout by a continuous sheet of mesodermal epithelium, the peritoneum; organs and structures that lie in the coelom are also covered by the peritoneal layer and are suspended by double mesodermal sheets, the mesenteries. In *C*, the peritoneum and mesenteries are represented by broken lines.



1. PORIFERA
   No true symmetry
   Diploblastic (?)
   No true tissues
2. COELENTERATA and CTENOPHORA
   Radial to bilateral
   Diploblastic to triploblastic
   Tissues, no true organs
3. PLATYHELMINTHES
   Bilateral
   Triploblastic
   Non-segmented
   Acoelomate
   Organs and organ systems
4. MOLLUSCA
   Bilateral
   Triploblastic
   Non-segmented
   Eucoelomate
   Organ systems
5. ANNELIDA
   Bilateral
   Triploblastic
   Segmented
   Eucoelomate
   Organ systems
6. ECHINODERMATA
   Secondarily radial
   Triploblastic
   Non-segmented
   Eucoelomate
   Organ systems
7. CHORDATA
   Bilateral
   Triploblastic
   Segmented
   Eucoelomate
   Organ systems

Fig. 7.6. Summary of general characteristics of major animal groups.

like **Vermes**. Later, the Vermes were partitioned into several smaller phyla. Again, Cuvier's Radiata were split into the phylum **Echinodermata** and the phylum **Coelenterata**, and later the phylum **Porifera** was separated from the coelenterates. Thus, more knowledge has made more phyla, although a limit has apparently been reached in such groups as the Chordata, Arthropoda, Mollusca, and Echinodermata, with their clearly defined characteristics (Fig.

7.6). There are always differences of opinion among the experts, even when the same observations are involved, and many aspects of classification must remain matters of judgment until more explicit information is forthcoming than any now available. Yet, there has come to be an increasing degree of agreement in taxonomy as knowledge of animal life and characteristics has progressed.

Evolutionary Interpretation of Classification. We may now examine the evolutionary implications of the natural or genetic classification, which zoologists have constructed on the basis of structural resemblance. This classification is, as we have seen, an effort to construct a family tree of animal life. If certain phyla are placed together as Eumetazoa, the grouping means that they are regarded as closely related in ancestry. It is possible, therefore, to consider classification as **a statement of evolutionary probabilities.**

Referring to Figure 7.4 as though it were a family tree, we may state that the first great step in evolutionary progress of animals was the divergence between forms that continued in the ancestral single-celled condition and gave rise to the Protozoa, and those that attained in some way the multicellular state and gave rise to the Metazoa. Within the latter line, the next major divergence was between animals that continued in a primitive state of differentiation, the Mesozoa and Parazoa, and forms that acquired a gut cavity, along with other complexities, and became the progenitors of all the eumetazoan phyla. Within this more advanced group next occurred a divergence into two stems: one, developing radial symmetry, the Radiata, and the other, with bilateral symmetry, the Bilateria. Again, within the great stem Bilateria, forms possessing a body cavity arose from ancestors which had lacked such a cavity; and this space evidently originated in various ways and became variously specialized. Finally, we have come in the course of evolution to the existing phyla with their subdivisions, and to the species and individual animals of today.

Many of these animals, in their fullest, adult development, resemble forms which may be interpreted as having served as stages in the evolution of higher animals. This existence, in the life cycles of complex forms, of developmental stages which resemble those of much simpler animals is considered significant in evolutionary interpretation and is the basis of the so-called **Recapitulation Theory.** This states, in essence, that in its own developmental sequence each individual organism exhibits transitory stages which represent stages in the evolutionary history of the group to which it belongs. According to this theory, we should be able, within certain limits, to determine the phylogenetic derivation of a group of animals by studying the embryonic development of modern representatives of the group. Interpreted in this light, the existence of a unicellular stage, the zygote, in the life cycle of every sexually reproducing animal may be regarded as reflecting the probability that all multicellular animals have descended ultimately from unicellular forebears. The fact that all members of the phyla grouped as Bilateria (Fig. 7.4) exhibit in some degree the so-called gastrula stage in their life cycles may be taken to indicate that a two-layered condition, which now persists in the adult stage in the simplest coelenterates and as a developmental stage in higher animals, was characteristic of the cômmon ancestors of Radiata and Bilateria. Whatever its evolutionary significance, the gastrula is morphologically a two-layered sac, generally comparable with the basic type of structure in simple coelenterates. Similar interpretations may be based on the appearance of fish-like stages in the development of amphibians and higher vertebrates, and on the existence of various stages of development within other phyla which are suggestive of ancestry. It should be emphasized, however, that no existing species of animal is regarded as the specific ancestor of any higher group.

The grand course of evolution can be pictured if we speculate on the changes that have occurred since the differentiation of organisms into animals and plants. It is clear that the major steps in this great progression occurred at a very early period, since the oldest fossil remains of animals, in rocks of the Pre-Cambrian period (older than 500 million years), include types representing all the great phyla except the Chordata. The conclusions presented graphically by the family tree in Figure 7.3 are frankly speculative; they are based on facts of structure and development observed in living animals or are deduced from comparisons of fossil remains, interpreted in the manner just described.

CHAPTER 8

CHAPTER **8**

UNICELLULAR ANIMALS:

The Protozoa

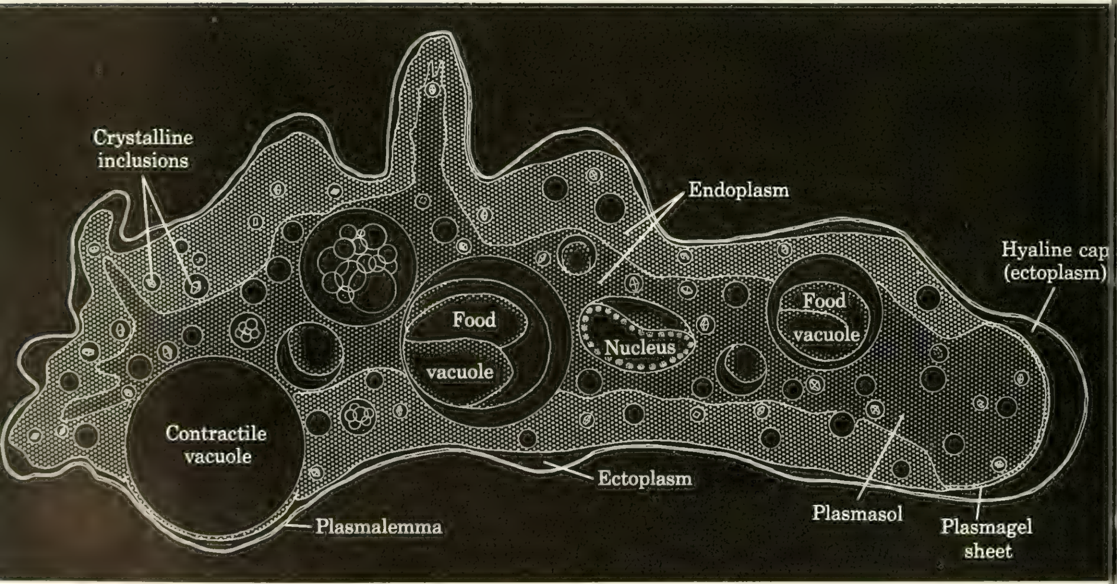

Crystalline inclusions
Endoplasm
Hyaline cap (ectoplasm)
Food vacuole
Nucleus
Food vacuole
Contractile vacuole
Ectoplasm
Plasmalemma
Plasmasol
Plasmagel sheet

Fig. 8.1. *Amoeba:* general structure; schematic optical section. (Adapted from S. O. Mast, 1925, *Journal of Morphology and Physiology,* vol. 41, printed by permission.)

In the preceding discussion of the classification of animals, it was pointed out that the simplest animals are unicellular, and that on the basis of this characteristic they may be classified as members of the subkingdom **Protozoa**, containing only the phylum **Protozoa**. These unicellular animals may be contrasted with all the phyla of multicellular animals constituting the subkingdom **Metazoa**. The Protozoa are defined as single-celled animals, although some protozoans form permanent colonial aggregations which approach the simplest metazoans in complexity. The word Protozoa ("first animals," "primordial animals") is well chosen; although many protozoan cells are very highly specialized, the single-celled condition is considered most primitive of all the structural plans of animals. It seems reasonable to conclude that the protozoans have descended, without changing their unicellular state, from the primeval organisms that were also the ancestors of the Metazoa.

The phylum Protozoa is divided into two subphyla: the subphylum **Plasmodroma**, which contains the class **Sarcodina**, the class **Flagellata**, and the class **Sporozoa**; and the subphylum **Ciliophora**, which includes the most complex of the protozoans, along with many simpler types, in the class **Ciliata** and the class **Suctoria**.

The vast majority of protozoans are free living, but all members of the class Sporozoa are parasitic, and there are many parasitic species in other classes. Some of these parasites, such as the malaria organism, cause serious diseases in man and animals.

Save for exceptional species, the Protozoa are of microscopic size; for this reason, among others, they were not clearly understood in relation to other forms of life until rather late in the history of classification. Certain of the ciliates were observed and recognizably described by Leeuwenhoek as early as 1675, and many other protozoans were discovered during the eighteenth and nineteenth centuries. The unicellular nature of these animals, and the fact that they might be compared with the cellular units of metazoans, was not recognized until 1845, after the elucidation of the Cell Theory. Although we do not now speak of digestive tracts and other organs in protozoans, as Ehrenberg did in 1838, it must be recognized that within the limits of the unicellular state some protozoans are very complex organisms.

The structural complexity of many protozoans illustrates the fact that differentiation in animals may occur at the cellular level as well as in tissues or organs composed of large numbers of cells. The component cells of metazoans, specialized to carry on particular functions, are **physiologically unbalanced**. They can exist in such a state of specialization only because the many-celled organism taken as a whole is a physiologically balanced unit. The single cell constituting the body of a protozoan necessarily performs all functions, and hence it must be **physiologically balanced**, whatever its degree of specialization. Together with the complexity of many protozoans, this condition of physiological balance, which enables the protozoan to be a complete and independent individual, has led some zoologists to regard the Protozoa as animals to which the cell concept does not apply. According to this view, the Protozoa should be considered as **acellular**, or non-cellular, animals—as organisms whose bodies are not equivalent to individual cells but are simply not subdivided into cells.

Their minute size and soft bodies have made it impossible for most types of protozoans to leave any record as fossils. However, the siliceous skeletons of representatives of the group known as Radiolarians are found abundantly in Pre-Cambrian rock (considerably older than half a billion years) as well as in later deposits. These unicellular animals have thus had an extremely long evolutionary history.

In this chapter, the Protozoa will be examined as a phylum of the Animal Kingdom and as animals whose unicellular organization may be contrasted with the multicellular organization described for the vertebrates. Also, the capacities of metabolism, responsiveness, and reproduction, which are characteristic of all living things, will be examined and compared in protozoans and in vertebrates.

The Sarcodina

In the class **Sarcodina** are included the morphologically simplest forms of Protozoa, although from an evolutionary standpoint the Flagellata as a group are probably the more primitive. A distinctive feature of the Sarcodina is the capacity to form temporary protoplasmic extensions of the body, called **pseudopodia** ("false feet"). In the subdivision **Rhizopoda**, which includes creeping forms such as *Amoeba*, the pseudopodia are lobular or root-like, sometimes subdividing, and may frequently change their shape or be withdrawn. In the **Actinopoda**, which are floating forms such as *Actinophrys*, the processes are stiff, rod-like, and more nearly permanent. The name Sarcodina was first applied because protozoans of this class resemble undifferentiated protoplasm, which was originally termed "sarcode," or flesh. Notable among the Sarcodina are the genus *Amoeba* and related genera, which are collectively spoken of as amoebae or amoebas.

The Amoeba: *General Structure.* The protoplasm of an amoeba (Fig. 8.1) consists of a thin external layer, the **plasmalemma**, which functions as a cell membrane; a non-granular region just within, the **ectoplasm**; and a granular inner region, the **endoplasm**, in which the **nucleus** lies. Features of cells like those of a vertebrate are thus apparent. The larger bodies distributed in the cell body, or **cytosome**, are **granules** of various sizes, **food vacuoles** in which digestion occurs, a single **contractile vacuole**, and other vacuoles containing watery fluid and comparable with those found in many other cells. Also present are **crystals** of definite forms, which may be distinctive for particular species of amoebas; **oil globules**; and many small **inclusions** ranging to the limits of microscopic visibility. The significance of these parts will be discussed as necessary in the accounts to follow.

Movements and Responsiveness. The manner in which an amoeba moves, by the flowing of its irregularly shaped body, has attracted attention ever since the animal was studied by the early microscopists, who called it the **proteus animalcule**, or "changing little animal." This **amoeboid movement** is simple in appearance, but it is surprisingly difficult to explain. Some of its features can be imitated by inanimate models, such as a drop of clove oil in a mixture of glycerin and alcohol; here changes in surface tension are responsible for the phenomena, and one theory assumed that similar forces were significant in amoeboid movement. However, it is now clear that the movements of inanimate models are not strictly comparable with those of an amoeba. Various accounts have been given of the changes to be observed in the formation of pseudopodia and in the locomotion of different species. Amoebas have been described as extending their pseudopodia like jets of water from a fountain, with a current flowing outward in the center of a pseudopod and backward on all sides. They have been described as rolling like a sac with elastic walls and fluid contents; and they have been said to "walk" upon stiff pseudopodia. Different kinds of amoebas thus move in different ways, but the formation of pseudopodia is probably fundamentally similar in all. The best and most generally applicable theory of amoeboid

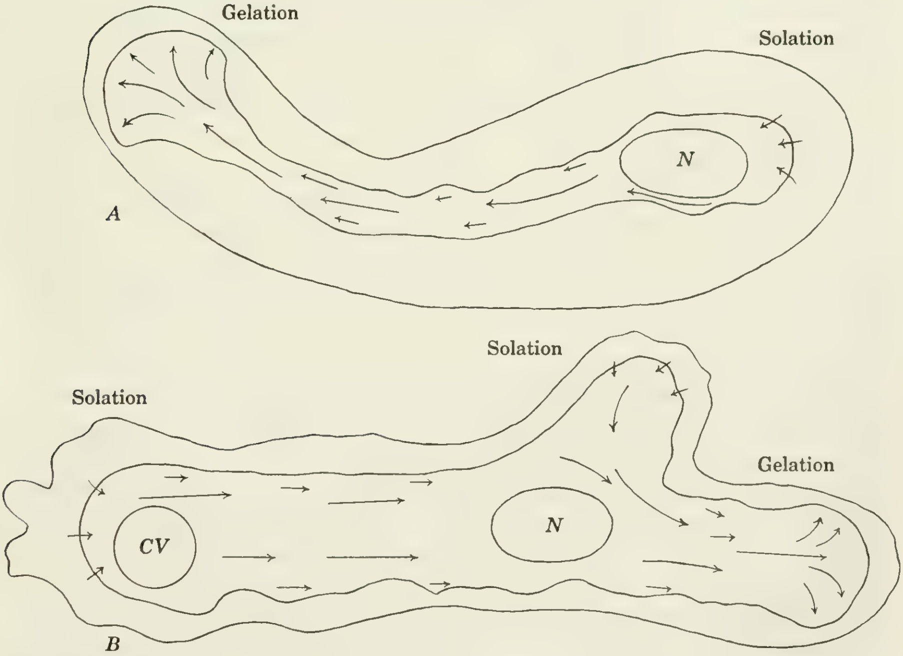


Fig. 8.2. *Amoeba:* cytoplasmic movements in locomotion. *N*, nucleus; *CV*, contractile vacuole. (Adapted from S. O. Mast, 1925, *Journal of Morphology and Physiology*, vol, 41, printed by permission.)

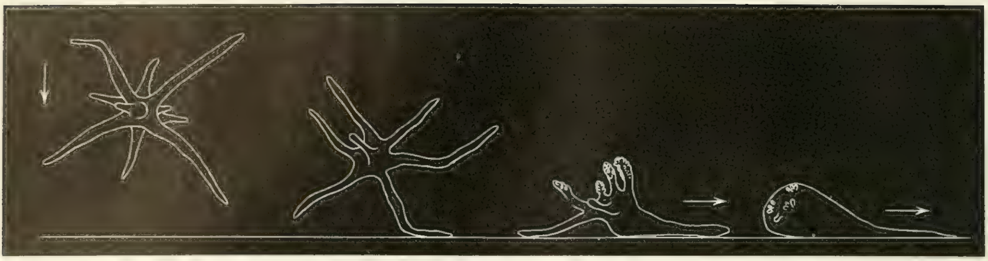


Fig. 8.3. *Amoeba:* reactions to contact with substratum. (Adapted from H. S. Jennings, *The Behavior of the Lower Organisms*, copyright 1906 by Columbia University Press, printed by permission.)

movement is based on the assumption that a relatively stiff, elastic layer, the **plasmagel**, surrounds the cell just beneath the plasmalemma and encloses the more fluid inner contents, or **plasmasol** (Fig. 8.2). Localized changes cause a temporary liquefaction of the gelatinous outer layer at the point where a pseudopod is to arise; the elasticity of the remainder of the gelatinous sheath forces the fluid endoplasm against and through such a weakened area. Within the pseudopodial lobe thus formed, the fluid endoplasm flows peripherally and stiffens, adding to the plasmagel layer. This type of movement, therefore, involves one of the fundamental capacities of the endoplasm: that of changing its physical state from **gel** to **sol**, and the reversal of this process. An amoeba, we may say, moves as a tunnel might, if the mortar of its wall became fluid at the posterior end and flowed within the tunnel to its anterior end, carrying the bricks to be laid again anteriorly by a new setting of the mortar.

Just as the collective reflexes make up the behavior of multicellular organisms such as vertebrates (see p. 86), the movements and other reactions of an amoeba in response to stimuli, or changes in the environment, make up the behavior of this unicellular animal. We may compare the activities of the single-celled amoeba with those of a white blood cell in the vertebrate body (see p. 63), or we may think of the amoeba as an individual animal to be compared with another complete individual. In the former case, we compare cell with cell, and the parallels are obvious. In the latter comparison, we forget about the cellular organization and think only of the individual as a whole. The behavior of white blood cells, when they move into certain regions and ingest such foreign bodies as bacteria, may be compared with the behavior of amoebas. The behavior of other cells in the vertebrate animal may be similarly compared, but the correspondence is less evident.

Thoughtful consideration of an amoeba as an individual, reacting to its environment, and in comparison with another individual, such as the many-celled vertebrate, enables us to recognize broad factors common to each, and to state them in general terms, irrespective of the cellular organization of either animal. Nevertheless, what is called the behavior of an amoeba is based on the capacity of **responsiveness**, as shown by the reactions of a single independent cell. The behavior of a multicellular animal is also based on the responsiveness of cells, but such behavior involves reactions in sequence by a number of cells.

Most easily demonstrable reactions of amoebas are negative, since they consist of withdrawals of pseudopodia or contraction of the cell in response to stimulation. Certain other responses, to contact, for example, are positive reactions. An amoeba dropped into water and settling slowly toward the bottom through a considerable distance may give a positive response by extending pseudopodia in all directions (Fig. 8.3). If one of these pseudopodia comes into contact with a surface, such as the stem of a water plant, the amoeba may respond positively by flowing in the direction of this contact and may thus begin to move over the surface. If one of its pseudopodia is then touched with a glass needle, or if certain chemicals in solution are brought into contact with a pseudopod by means of a capillary pipette, a negative response may be indicated by withdrawal of the pseudopod. If the stimulus is sufficiently strong, the entire amoeba may contract into a globular form. Positive reactions are also involved in feeding, and these will be described in the account of metabolism which follows.

Feeding and Metabolism. Amoebas feed upon other organisms, both animal and plant, and may thus be described as **holozoic** in their nutrition. Such a species as *Amoeba proteus* is essentially a beast of prey, eating whatever it can capture, from small to relatively large protozoans and single-celled plants. The most common food of this species consists of small flagellates and ciliates, which an amoeba consumes in large numbers. **Ingestion** involves the extension of pseudopodia about the prey, which is engulfed and transferred into the endoplasm (Fig. 8.4). A **food vacuole** thus originates by the enclosure of a drop of water containing one or more food bodies. The feeding reactions are surprisingly complex and variable, considering the apparent simplicity of an amoeba. Forms such as motionless unicellular plants evoke responses different from those induced by active prey. A certain selec-

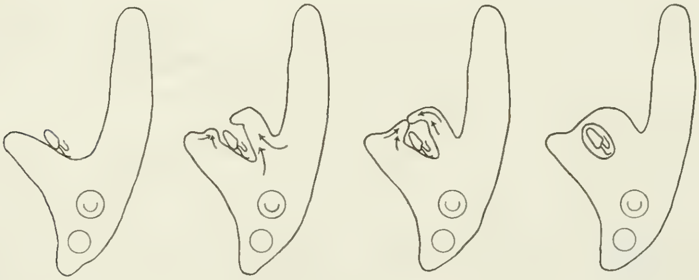


Fig. 8.4. *Amoeba:* ingestion of a flagellate and successive stages in the formation of a food vacuole. (Adapted from W. A. Kepner and W. H. Taliaferro 1913, *Biological Bulletin*, vol. 24, printed by permission.)

tivity is exhibited by the amoeba: in the presence of two kinds of prey, equally abundant, the organism ingests the one kind which appears to be most easily digested, and rejects the other. Moreover, the responses are not fixed and mechanical but vary with the physiological state of the amoeba. In the adjustment of reaction to stimulus, and to the state of its physiology, an amoeba behaves in a manner resembling the behavior of multicellular organisms.

The resemblance between the vital functions in an amoeba and those in a vertebrate may be shown by tracing the history of the ingested food. When a small flagellate, such as *Chilomonas*, is ingested by *Amoeba proteus*, the prey continues to move about for several minutes before it is killed by something within the vacuole. Meanwhile, the food vacuole, which at the outset contains a relatively large amount of water, shrinks by the diffusion of excess water into the cytoplasm. The fluid then remaining within the vacuole becomes alkaline, and in later stages it becomes acid. If the changes in individual vacuoles are followed, the *Chilomonas* will be seen to disintegrate gradually, until, some 12 or 24 hours later, there remain only certain granules that are apparently indigestible. Fat globules are liberated from the food mass and appear in the vacuolar fluid within 2 or 3 hours, after which they gradually decrease in size and disappear. Starch grains disintegrate into a pasty mass, which disappears as the vacuole slowly decreases in volume.

The disintegration of other particles and further shrinkage of the vacuole follow, until only a few granules remain. Even these remnants may pass into the endoplasm instead of being egested. **Egestion** occurs by the discharge of food in various stages of digestion, and of the indigestible residue of food, after all the digestible material has passed into the cytoplasm. Often several vacuoles in late stages coalesce, and the resulting mass comes into contact with the plasmalemma at or near the posterior end of the amoeba. The mass is egested by rupture of this membrane. From observations such as these, it is inferred that fats, carbohydrates, and proteins are digested in the food vacuoles, presumably by specific enzymes, as in the digestive tracts of many-celled animals. It also appears that the products of digestion pass into the endoplasm as they pass into the cells lining the digestive tract of a higher animal. Alternatively, the comparison may be made with the absorption of nutrients from the surrounding lymph by cells in all parts of the vertebrate body. Thus, the digested food is ready to be **assimilated.**

Amoebas cannot survive in water from which all dissolved oxygen has been removed, as by boiling; this demonstrates that available oxygen is necessary for the continued existence of these animals. Normally, oxygen diffuses into the cell from solution in the surrounding medium, just as it enters the cells of a vertebrate from solution in the intercellular lymph. As in the cells of vertebrates, oxygen is essential to cellular metabolism, the series of oxidative reactions which release energy within the cell. The end products of the catabolic process are, as in the vertebrate, carbon dioxide, water, and nitrogenous compounds. These are eliminated from the amoeboid cell by **excretion** through its surface. Excretion in *Amoeba* may be compared, again, either with that of a component cell of a higher animal, or with that of the higher animal as an organism. For in a vertebrate excretion occurs initially at the cellular level, waste products being released by cells into the lymph, eventually to find their way to the specialized organs of excretion through which they will ultimately be eliminated from the body. At the amoeba's unicellular level of organization, the initial passage of wastes from the cell into the surrounding water completes the process of excretion.

The **contractile vacuole** of Protozoa has long been considered as primarily an **organelle** (the intracellular counterpart of a multicellular organ) specialized for the elimination of excreta. Nitrogenous substances have actually been detected in samples of fluid ingeniously removed from contractile vacuoles. However, the chief function of these structures probably involves the removal of excess water from the cell. As a result of the osmotic gradient between the external medium and the cell contents, water tends constantly to enter the cell, and provision must be made for its elimination. The contractile vacuole may be thought of as a pump, operating continuously to maintain the proper environmental conditions within the cell. The water removed by this action contains a certain amount of excretory material in solution, and to this extent the contractile vacuole may be regarded as an excretory organelle. Many protozoans (for example, most marine forms) lack contractile vacuoles and must depend entirely on diffusion through the general cell surface for the elimination of wastes. Undoubtedly most excreta are removed from *Amoeba* in this manner.

From these considerations it is apparent that the metabolic processes of this very simple, unicellular animal and of a complex vertebrate are essentially analogous. The fundamental requirements of both protozoan and metazoan cells are everywhere comparable: food, providing energy sources and essential basic substances; oxygen, for the combustion of nutrients in an ordered manner, releasing energy for synthetic activities; and a provision for the maintenance of favorable internal conditions by the elimination of metabolic wastes. The chief differences displayed concern the fact that in each species the cell synthesizes the particular specific compounds characteristic of its kind.

Life Cycle and Reproduction. The life cycle, or life history, of a many-celled animal is the series of changes from egg to adult that occurs in each generation. Many protozoans, including some members of the Sarcodina, also exhibit serial changes of form which constitute their life cycles. In the common amoebas, however, the life history seems to involve nothing but an endless

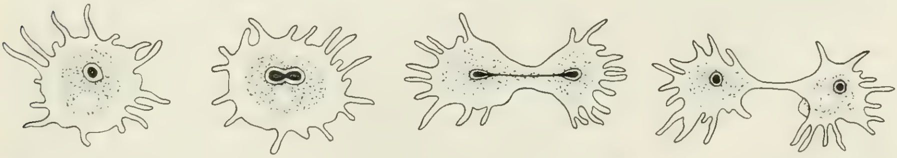


Fig. 8.5. *Amoeba:* successive stages in division. (Adapted from K. von Frisch, 1952, *Biologie*, vol. 1, printed by permission of Bayerischer Schulbuch-Verlag.)

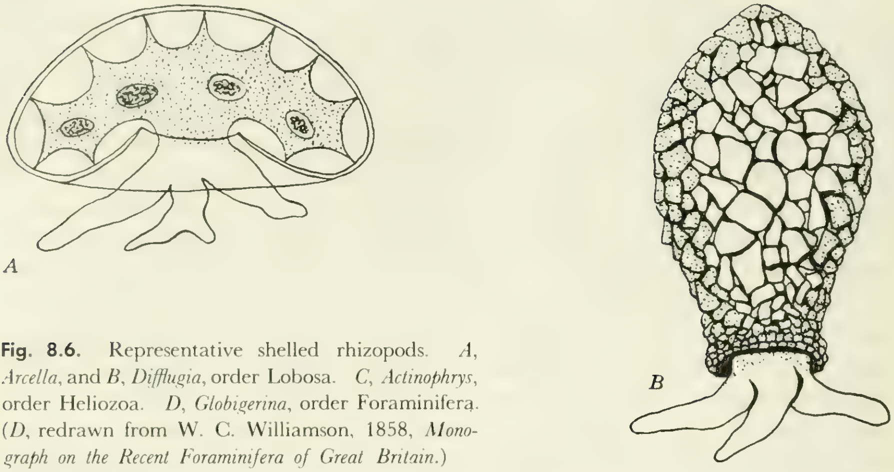
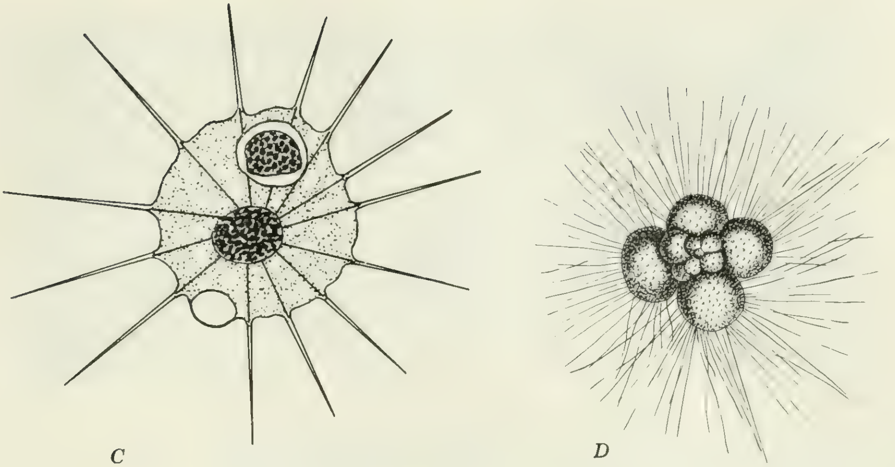


Fig. 8.6. Representative shelled rhizopods. *A*, *Arcella*, and *B*, *Difflugia*, order Lobosa. *C*, *Actinophrys*, order Heliozoa. *D*, *Globigerina*, order Foraminifera. (*D*, redrawn from W. C. Williamson, 1858, *Monograph on the Recent Foraminifera of Great Britain.*)

series of cell division by **binary fission**, although more complicated phenomena, such as encystment and sexual reproduction, have been described. Present indications are that *Amoeba proteus*, for example, reproduces only by binary fission (Fig. 8.5), with subsequent growth of the daughter cells to full size, continuing in the active state without syngamy or encystment. Amoebas may become smaller through starvation, or, as in some larger species, multinucleate forms may be produced by the failure of the cytosome to divide following nuclear division. The large fresh-water amoeba, *Pelomyxa carolinensis*, contains hundreds of nuclei produced in this way. At the time of cell division, the cytosome divides, distributing the nuclei between the resultant daughter individuals. In some of the other amoeboid forms, more complicated life cycles, with budding and encystment, have been discovered. Some of these cycles include flagellated stages, and in others, gametes and syngamy are known.

Other Sarcodina. The genus *Amoeba*, with many other free-living forms which it resembles, is placed in a subdivision of the Sarcodina known as the **Rhizopoda.** Other rhizopods, such as the genera *Arcella* and *Difflugia*, possess shells with a single opening from which the pseudopodia extend (Fig. 8.6). In the Foraminifera, there is a shell composed of calcium carbonate, chitin, silica, or other materials, and the pseudopodia extend through numerous openings. With few exceptions, the Foraminifera are marine, living near the surface of the sea as well as on the bottom. The shells of dead foraminiferans make up a large part of the silt that covers the ocean floor, in regions such as the deeper portions of the North Atlantic. In chalk formations in various parts of the world, some of them hundreds of feet thick, these minute shells make up as much as 70 per cent of the deposits. Another subdivision, the **Actinopoda,** includes the "sun animalcules," such as *Actinophrys sol* (Fig. 8.6), and the **Radiolaria**, which are notable for their siliceous skeletons of great beauty and variety (Fig. 8.7). In some of the very ancient sedimentary rocks occur



skeletons of Radiolaria and Foraminifera almost identical with those of present-day species. This fact indicates that these forms, and so perhaps many other Protozoa, have remained almost unchanged for half a billion years or more.

Parasitic Rhizopoda. Although most of the rhizopods are free-living animals, a smaller number of the known species are parasitic. One of these, *Entamoeba histolytica*, causes the serious disease of humans called **amoebic dysentery**, or **amoebiasis**. *Entamoeba histolytica* is found in humans chiefly in the large intestine, where the active feeding stages, or **trophozoites**, destroy the mucous membrane and invade the submucosa. The ulcers of the intestinal lining thus formed become infected with bacteria, as well as with amoebas. The food of the parasite consists of the tissues it destroys, together with large numbers of red corpuscles. In advanced cases of amoebiasis, the parasite may gain access to the intestinal blood vessels; in the blood stream, the parasites are carried to the liver, lungs, and brain. Almost any part of the body may be thus invaded, the amoebas then causing serious abscesses in the secondary sites. Hence, the symptoms of amoebiasis are not limited to intestinal disturbances.

The trophozoites (Fig. 8.8) may be observed in the freshly discharged feces of the host. They become increasingly sluggish as the feces cool and die within a few hours. The feces of an infected individual also contain large numbers of **encysted stages** of the parasite, which are smaller cells encased in cysts and having typically four nuclei. The cysts can survive for some time outside the host and are moderately resistant to heat and cold. They can be killed by the pasteurization process in milk and by boiling in water. Viable cysts are transferred to the intestine of a new host via the mouth and digestive tract in contaminated food and drink, and to a lesser extent by other means. Reproduction in the trophozoite stage occurs by binary fission. In the en-

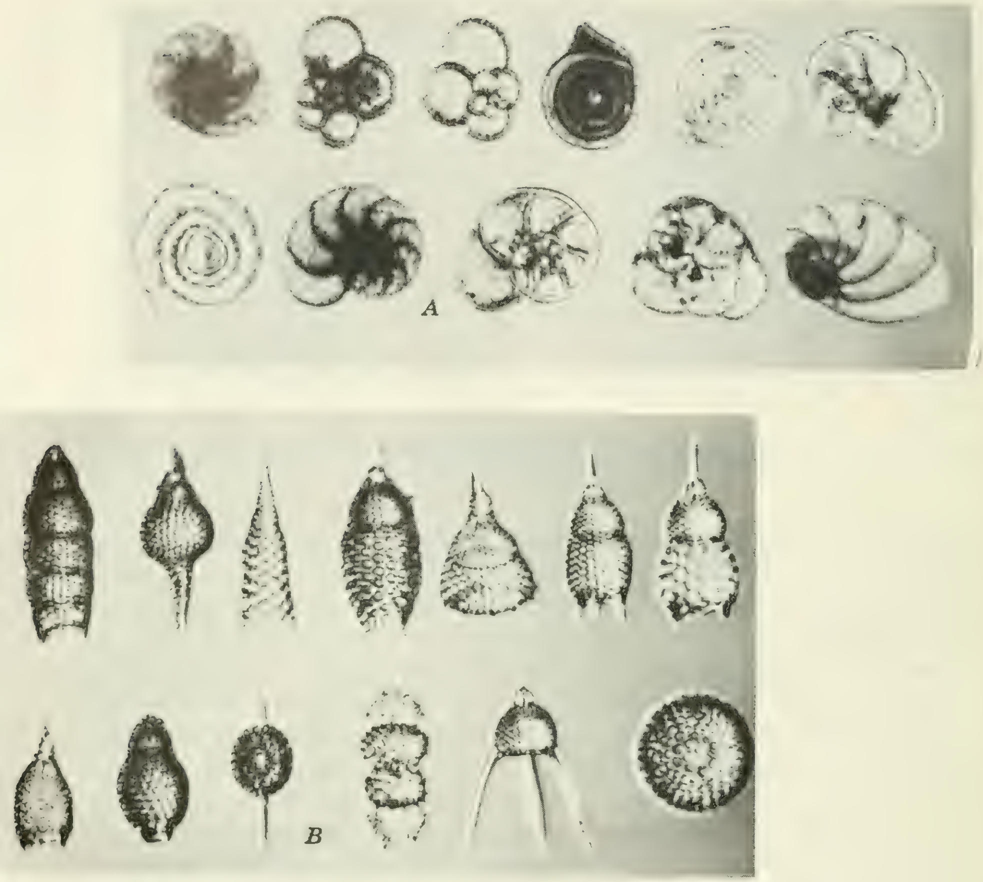


Fig. 8.7. Skeletons of representative foraminiferans (*A*) and radiolarians (*B*). (Photographs courtesy General Biological Supply House, Inc.)

cysted form, the four nuclei are produced by two nuclear divisions, the forerunners of cytoplasmic divisions which occur immediately after **excystment.** From each cyst, eight uninucleate individuals are ultimately produced, each of which subsequently grows into the large, active trophozoite form.

Once regarded as a tropical disease, amoebiasis is now known to be distributed throughout the world, even to the Arctic Circle. Infections are of common occurrence wherever crowded conditions are combined with inadequate sanitary facilities; such situations may lead to the outbreak of epidemics. With increasing travel to and from parts of the world where the incidence of the disease is high, amoebiasis may cause increasing concern in this country. Fortunately, methods of prevention are well known, although not always practiced; however, curative treatment is still a problem.

A variety of other amoebas inhabit the intestine of man and lower animals, probably more species than can now be recognized. Most of these appear to be relatively harmless "messmates," or **commensals**, living within the larger animal but not markedly disadvantageous to the host.

The Flagellata

In the class **Flagellata** are included the protozoans possessing one or more **flagella** (singular, flagellum), or whip-like extensions of the cytoplasm, during the more representative phases of the life cycle. Flagella are primarily organelles of locomotion; in some species they also assist in feeding. Flagella are also found in many species of Sarcodina but usually only during a limited part of the life cycle. In a similar manner, amoeboid stages occur in the life cycles of many flagellates. The existence of both flagellate and amoeboid stages in a single species suggests a close relationship between Sarcodina and Flagellata. The Flagellata also exhibit a close relationship with plants, since many of the flagellate Protozoa possess chlorophyll and are sometimes indistinguishable from unicellular plants. Among such plant-like flagellates are species of the genus *Euglena*.

The Euglena: ***General Structure.*** A typical euglena (Fig. 8.9) is covered by a thin **pellicle**, comparable with the cell wall in plant cells and often marked externally in a spiral pattern. The pellicle is stiff enough to preserve the contours of the organism as it swims through the water but flexible enough to allow the changes of shape called **euglenoid movement**. The anterior end of the organism bears a mouth-like notch, from which a flask-shaped cavity extends a short distance into the cell. The single **flagellum** protruding from this cavity arises from two branches, each of which originates in a granule, or **blepharoplast**. From one blepharoplast a fiber extends to the nuclear membrane. The flagellum itself consists of a central **axial filament**, formed by the union of the two branches, and a surrounding, spirally wound

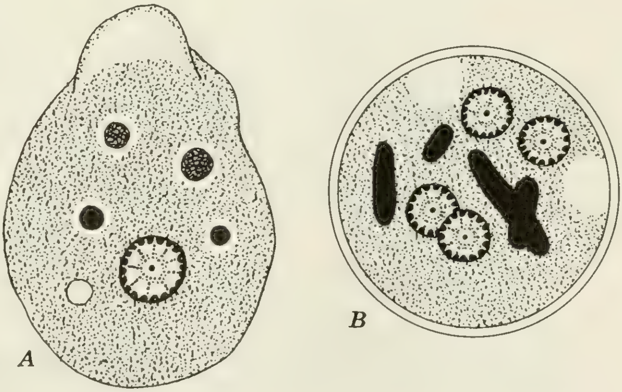


Fig. 8.8. *Entamoeba histolytica. A*, trophozoite or vegetative form; *B*, a cyst. (Adapted from W. Balamuth in F. A. Brown, Jr., *et al.*, *Selected Invertebrate Types*, copyright 1950 by John Wiley and Sons, Inc., printed by permission.)

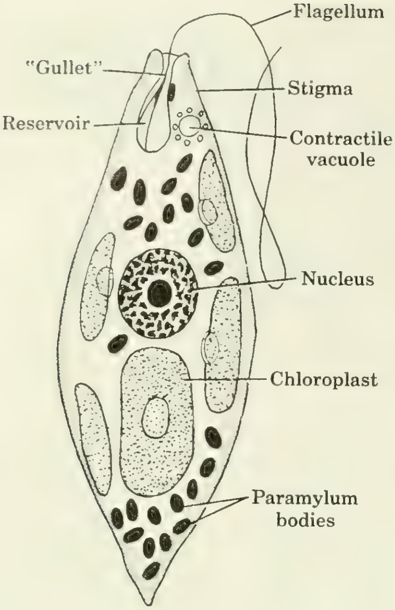

Flagellum
"Gullet"
Stigma
Reservoir
Contractile vacuole
Nucleus
Chloroplast
Paramylum bodies

Fig. 8.9. *Euglena viridis:* general structure. (Adapted from W. Balamuth in F. A. Brown, Jr., *et al.*, *Selected Invertebrate Types*, copyright 1950 by John Wiley and Sons, Inc., printed by permission.)

sheath. In *Euglena* the cavity from which the flagellum extends does not function as a mouth and gullet, for in its nutrition the euglena is **holophytic,** like the green plants. In related flagellates which ingest and digest food, the anterior opening may more properly be called a mouth. In the euglena, in the anterior end of the cell, minute vacuoles periodically enlarge and coalesce to form a **contractile vacuole,** which discharges into the "gullet." As in the

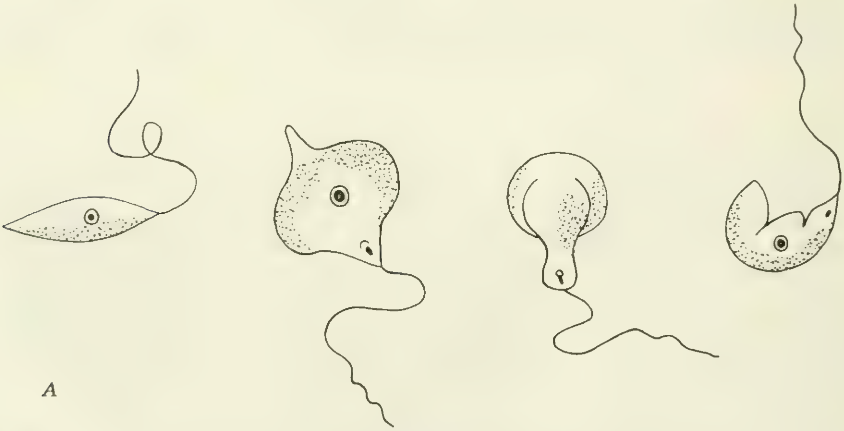


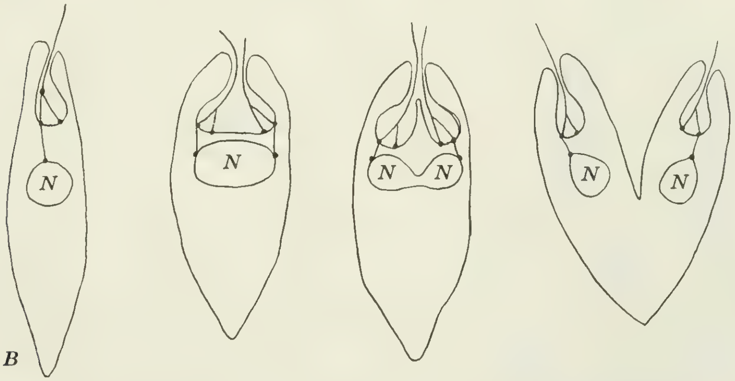
Fig. 8.10. *A*, euglenoid movement; note the extreme plasticity of the cytosome. *B*, binary fission in *Euglena viridis;* the division of the nucleus (*N*) involves a mitotic process. (*A*,

amoeba, such vacuoles are believed to eliminate water from the cell, and only incidentally to serve for the expulsion of the soluble excreta which this water may contain.

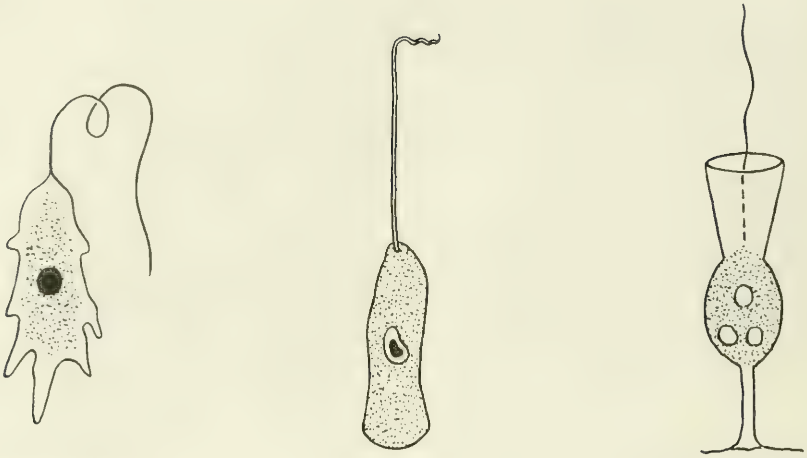
A mass of red pigment at the anterior end of the organism is called the **stigma**, or eye spot; it seems to be a light-sensitive organelle. The **nucleus** lies near the center of the cell, surrounded by green chromatophores, the **chloroplasts**, which fill the cytoplasm. The chloroplasts contain chlorophyll and are responsible for the green color of the cell. This chlorophyll is comparable with that in the green cells of plants. Between the chloroplasts the most conspicuous inclusions in the cytoplasm are bodies of characteristic shape, varying between different species, composed of **paramylum**. This is a complex carbohydrate related to starch, and the paramylum bodies are interpreted as stored food reserves. There is no flowing of the endoplasm as in the amoeba, although the plasticity of the cytosome is demonstrated when the euglenoid cell changes its shape.

Movements and Responsiveness. Characteristic expansions and contractions of the cell, occurring when the euglena is not in active locomotion, are called **euglenoid movements** (Fig. 8.10). These are not interpreted as related to progressive locomotion, which is brought about by the action of the flagellum. The flagellum beats in such a way as to propel the organism in a spiral course, rotating upon its long axis.

By these movements of the cell body, and by spiral swimming, the organism reacts to a variety of stimuli. The behavior with respect to light, a necessary factor in the environment of these plant-like forms, has been studied especially. Observations have shown that a euglena which has been moving toward a source of light gradually changes its direction when the direction of the light is changed and so continues to orient positively toward the light. The adjustment involves a complex series of movements, including rotation of the cell upon its long axis; but once the orientation is accomplished, the animal con-



after A. E. Shipley, 1893, *Zoology of the Invertebrata; B,* adapted from R. P. Hall and T. L. Jahn, 1929, *Transactions of the American Microscopical Society,* vol. 48, printed by permission.)



Mastigamoeba *Peranema* *Monosiga*

Fig. 8.11. Representative colorless flagellates. Although *Mastigamoeba* produces pseudopodia, it is considered a flagellate because of the presence of a flagellum. *Monosiga*, a choanoflagellate, bears a protoplasmic collar surrounding the flagellum.

tinues its spiral progression in one direction. In general, the euglena responds positively to light of optimum intensity; if the light is very intense, a negative response will be exhibited. In these and other reactions the organism manifests the **responsiveness** characteristic of all cells.

Nutrition and Metabolism. Possessing chlorophyll, the euglena carries on **holophytic** nutrition like that of green plants. It is doubtful that ingestion of food ever occurs in *Euglena*, although such colorless flagellates as *Peranema* and others do ingest small organisms through the gullet and form food vacuoles. When kept in darkness, *Euglena gracilis* and other green flagellates lose their green color but continue to live and reproduce for long periods. This is true, however, only if certain organic compounds are present in the culture medium, to satisfy the energy requirements of the cells. Thus it has been established that the same species can maintain itself in the light by holophytic nutrition and in darkness by **saprophytic** or **saprozoic** nutrition. In the absence of light, the organism is unable to manufacture its energy-rich compounds by photosynthesis and must depend on external sources.

Life Cycle and Reproduction. As in many other protozoans, the life cycle of some species of *Euglena* includes an **active phase**, during which the organism moves about, and an **encysted phase**, during which it is enclosed within a cyst and is non-motile. It is questionable whether *Euglena viridis* ever undergoes encystment. In this species reproduction occurs by **binary fission**, which is typically a longitudinal division beginning at the anterior end of the cell (Fig. 8.10). In other euglenas this division may proceed in either the active or the encysted phase. So far as is known, there is no sexual reproduction in flagellates like *Euglena*, although the production of gametes, and syngamy, are well known in other flagellates.

Other Flagellates. For convenience, the flagellates are sometimes subdivided into two groups, the plant-like and the animal-like forms. The class is so heterogeneous that such a major subdivision is of questionable value. Some of the plant-like forms are clearly very similar, structurally, to other species which lack chlorophyll. It is evident that the Flagellata are very difficult to separate from the unicellular plants, on the one hand, and from the Sarcodina, on the other; they also show some affinities with the Sporozoa, to be described later. The flagellates include many interesting forms (Fig. 8.11). In *Mastigamoeba* the cell is amoeboid, although the presence of a flagellum leads to its classification as a flagellate. In *Peranema* the cytosome is strikingly mobile, and the flagellum is generally held straight out anteriorly, vibrating only at the distal end as the animal progresses. In *Monosiga* and related forms, called **choanoflagellates,** there is a delicate protoplasmic collar surrounding the flagellum, and ingestion of food particles occurs in this region. *Noctiluca*, a dinoflagellate, is one of the organisms responsible for luminescence in the ocean.

Parasitic Flagellates. Many of the Flagellata are parasitic. The lower digestive tract of man and other mammals often harbors such forms, and almost any frog or tadpole will be found to have more than one species of flagellate in its large intestine. The digestive tracts of termites and wood roaches contain an amazing array of **Hypermastigida,** a group of flagellates with very numerous flagella (Fig. 8.12), which have been shown to perform an essential function in the digestion of wood by these insects; hence, these are not actually parasites in the accepted sense.

The forms called **trypanosomes** ("awl body") occur in the blood of vertebrates and the digestive tracts of invertebrates (Fig. 8.13). A trypanosome

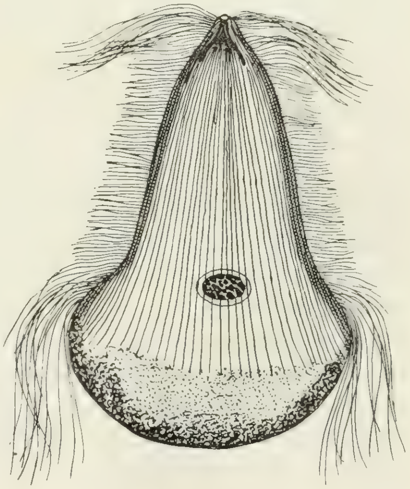


Fig. 8.12. A hypermastigote flagellate, *Trichonympha campanula*, from the alimentary tract of a termite. The longitudinal striae represent the lines of attachment of additional hundreds of flagella, with which the anterior portion of the organism is completely covered. (Adapted from C. A. Kofoid and O. Swezy, 1919, *University of California Publications in Zoology*, vol. 20, printed by permission of the University of California Press.)

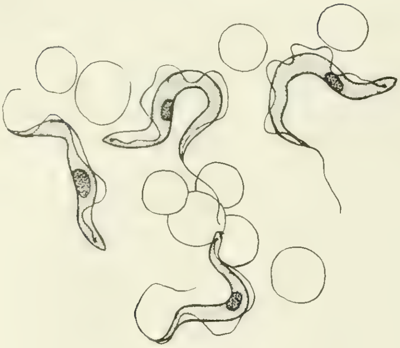


Fig. 8.13. *Trypanosoma gambiense*, the causative organism of one form of African sleeping sickness. The trypanosomes are shown as they appear in a smear of blood from an infected individual; the circles represent erythrocytes and indicate the relative size of the parasites.

is an elongated cell with an undulating membrane along one side, bounded laterally by an attached flagellum. The flagellum springs from a granule in the posterior end of the cell and becomes free anteriorly. A representative example is *Trypanosoma gambiense*, which causes one type of sleeping sickness so dangerous to man in equatorial Africa. By the bite of the bloodsucking tsetse fly, the stages of the parasite found in human blood are transferred to the intestine of this insect, which serves as the intermediate host. Here a series of reproductive stages occur; some 3 to 4 weeks later the parasites appear in the salivary glands of the fly, from which they may again be transferred to the blood of man or other mammals. In the final stages of parasitization, the trypanosomes invade the cerebrospinal fluid of the host, inducing the stupor that characterizes the disease and finally ends in death. Although these parasites produce a fatal disease in man, they cause no obvious ill effects in other hosts among the larger African mammals. Such a contrast in susceptibility may perhaps be explained on the theory that the wild mammals in question have become tolerant of the infection or have developed an immunity to its effects, as a result of natural selection acting upon very many generations. Man, on the other hand, has only comparatively recently come into contact with these parasites and is very susceptible.

The Sporozoa

The class **Sporozoa** contains only parasitic species. In correlation with this mode of life, the locomotor and other structures necessary in free-living animals are much reduced. The name Sporozoa ("seed animals") was given because "seed-like" stages, or **spores**, are conspicuous in the life cycles of these protozoans. Representative examples are species of the genus *Monocystis*, which inhabit the seminal vesicles of earthworms. The full-grown individual is an elongated cell with a single nucleus. This organism is capable of a slow, gliding locomotion by local contractions and extensions of the cell, but there are no complex locomotor structures or behavior. *Monocystis* is first

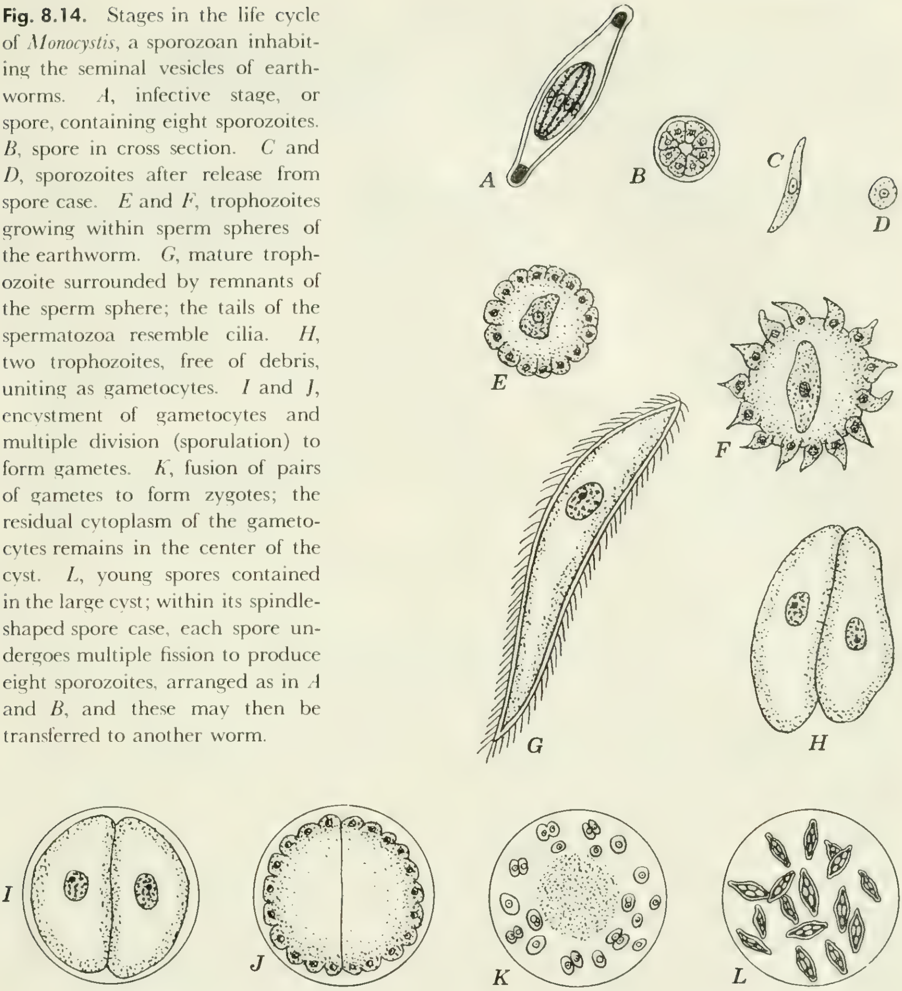


Fig. 8.14. Stages in the life cycle of *Monocystis*, a sporozoan inhabiting the seminal vesicles of earthworms. *A*, infective stage, or spore, containing eight sporozoites. *B*, spore in cross section. *C* and *D*, sporozoites after release from spore case. *E* and *F*, trophozoites growing within sperm spheres of the earthworm. *G*, mature trophozoite surrounded by remnants of the sperm sphere; the tails of the spermatozoa resemble cilia. *H*, two trophozoites, free of debris, uniting as gametocytes. *I* and *J*, encystment of gametocytes and multiple division (sporulation) to form gametes. *K*, fusion of pairs of gametes to form zygotes; the residual cytoplasm of the gametocytes remains in the center of the cyst. *L*, young spores contained in the large cyst; within its spindle-shaped spore case, each spore undergoes multiple fission to produce eight sporozoites, arranged as in *A* and *B*, and these may then be transferred to another worm.

an intracellular parasite and later lies free in the fluid of the seminal vesicle. Presumably, food is absorbed through the cell membrane from the surrounding medium, and metabolic wastes are eliminated by diffusion. An abundant reserve of nutrients is stored in the cytoplasm and is utilized during encysted and gamete-forming stages. The life cycle, shown diagrammatically in Figure 8.14, contains a stage in which rapid, successive divisions produce a large number of spores. This type of proliferative division, termed **multiple fission**, is a characteristic feature of the life cycles of all sporozoans.

Other representative Sporozoa may be listed as follows: species of the genus *Gregarina*, common in the digestive tracts of insects; the **coccidians**, which parasitize vertebrates and invertebrates and are exemplified by the genus *Eimeria;* and the **malaria parasites.**

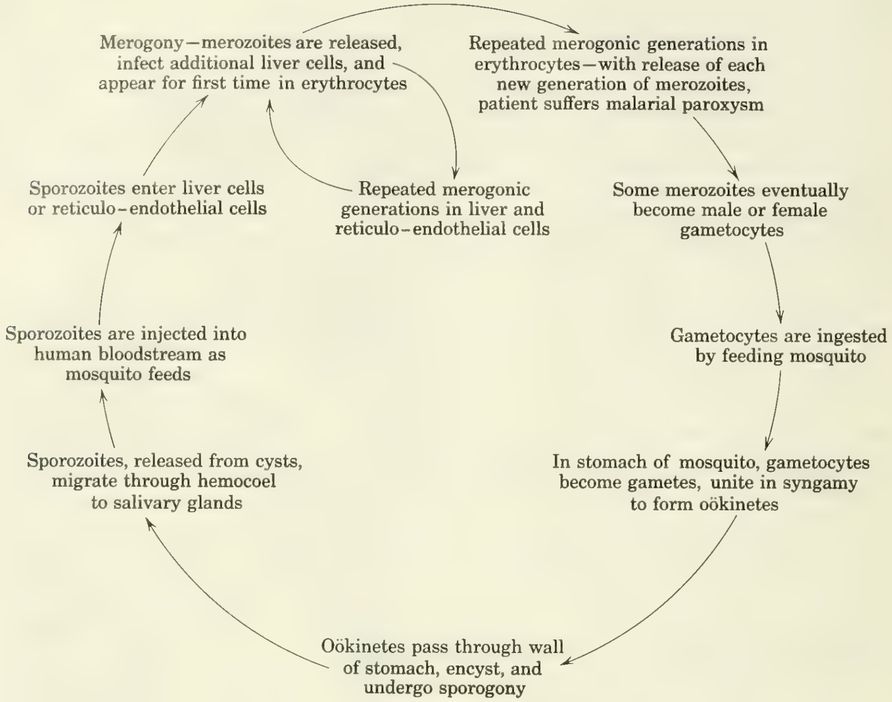

Merogony—merozoites are released, infect additional liver cells, and appear for first time in erythrocytes
Repeated merogonic generations in erythrocytes—with release of each new generation of merozoites, patient suffers malarial paroxysm
Sporozoites enter liver cells or reticulo-endothelial cells
Repeated merogonic generations in liver and reticulo-endothelial cells
Some merozoites eventually become male or female gametocytes
Sporozoites are injected into human bloodstream as mosquito feeds
Gametocytes are ingested by feeding mosquito
Sporozoites, released from cysts, migrate through hemocoel to salivary glands
In stomach of mosquito, gametocytes become gametes, unite in syngamy to form oökinetes
Oökinetes pass through wall of stomach, encyst, and undergo sporogony

Fig. 8.15. Sequence of events in the life cycle of the malaria parasite.

Malaria and the Malaria Parasite. The disease called malaria has been known since ancient times. Some investigators have regarded it as largely responsible for the decline of ancient Rome. It is certain that both Romans and Greeks, and probably other peoples, suffered greatly from this pestilence. Early explorers of the Americas found it established in the tropical regions of both continents and brought back to Europe the South American Indians' remedy, "peruvian bark" of the cinchona tree, from which quinine was later extracted. Intensive research, stemming largely from the shortage of this natural remedy during the years of World War II, has led to the production of new and more effective synthetic malaricides. The disease is still prevalent and serious, however, in all the warmer parts of the world.

The word malaria ("bad air") was originally applied to a group of fevers associated with swampy regions. The idea that the air of such a region acts as a causative agent is still prevalent among the ignorant. If there are no mosquitoes to act as intermediate hosts for the parasite, however, there is no malaria. The agents of infection in this instance are Sporozoa, various species of the genus *Plasmodium; Plasmodium malariae*, for example, produces one form of malaria in man. In the vertebrate host, the parasite lives intracellularly in the red blood cells and other cells, where asexual reproduction occurs by multiple fission or **merogony**. The resulting new generation of parasites (**merozoites**) are liberated with the destruction of the invaded erythrocytes, and in turn enter new cells in which the process is repeated. In this manner a very large number of erythrocytes may be destroyed and the population of the parasites greatly increased. In the form of the disease produced by *P. malariae*, the patient suffers chills and fever which recur at intervals of about 72 hours. This periodicity coincides with the maturation and liberation of successive generations of merozoites in the red cells, and it is probable that the symptoms are precipitated by the toxins released by the disintegrating cells. After a considerable period of such asexual reproduction, the parasite forms **macrogametocytes** and **microgametocytes**, which remain in the red cells of the vertebrate host until the blood is ingested by a mosquito. In the stomach of this host the gametocytes differentiate into **macrogametes** and **microgametes**, and syngamy occurs. The resulting motile **zygote** (oökinete) passes through the epithelium of the gut and takes up a position on the outer surface of the mosquito's digestive organs, where it becomes invested by a cyst wall. Within this cyst multiple fission again occurs, and eventually many spindle-shaped cells, the **sporozoites**, are formed. The cyst wall finally bursts, and the sporozoites thus liberated into the mosquito's body cavity migrate into its salivary glands. Here they remain until ejected with saliva when the mosquito bites a human. The life cycle of the malaria parasite is outlined in Figure 8.15.

A long-standing problem in malariology has been posed by the fact that within half an hour of the injection of sporozoites into the blood stream, they disappear from the circulating blood. Infected erythrocytes cannot then be found until some days later, when the symptoms of the disease begin to appear. It has recently been discovered that injected sporozoites do not penetrate erythrocytes but attack fixed tissue cells of the spleen, liver, and bone marrow (Fig. 8.16). Within these cells merogony proceeds, producing thousands of merozoites from each original sporozoite. Only after this "exo-erythrocytic" period of incubation are the erythrocytes of the circulating

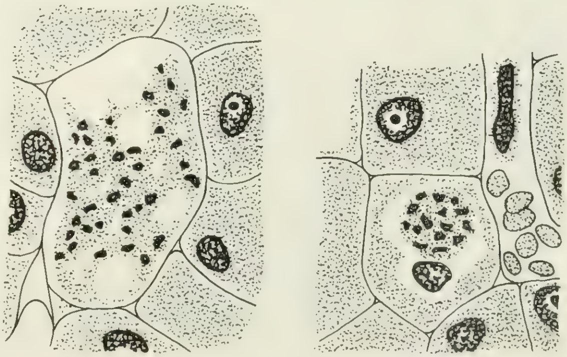


Fig. 8.16. Merogony in the exo-erythrocytic stages of *Plasmodium cynomolgi*, in liver cells of a monkey. The resulting merozoites will invade other liver cells, as well as erythrocytes, and in these fixed tissue cells will persist as a chronic source of infection. (Adapted, after H. E. Shortt, from R. P. Hall, *Protozoology*, copyright 1953 by Prentice-Hall, Inc., printed by permission.)

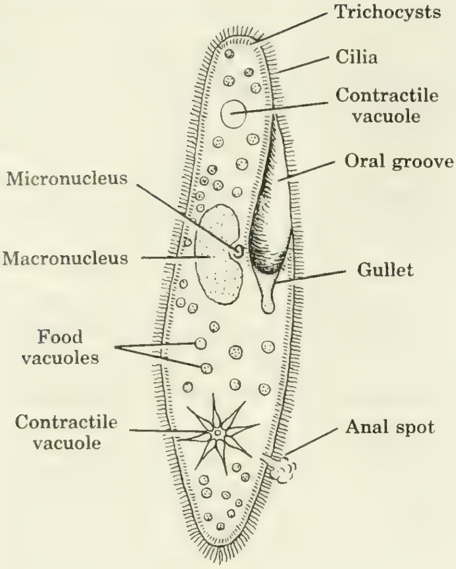


Fig. 8.17. *Paramecium:* general structure. (Adapted from L. H. Hyman, *The Invertebrates: Protozoa through Ctenophora*, copyright 1940 by McGraw-Hill Book Co., Inc., printed by permission.)

blood invaded. It has also been established that chronic infections may persist in the tissue cells after the blood has been cleared of parasites by treatment; this fact explains the frequent "relapses" often characteristic of the disease and the difficulty of effecting a final cure.

The Ciliata

The class **Ciliata** includes the protozoans in which the body is wholly or partially covered by cilia. Many of the ciliates are complex and highly specialized cells, whose structural complexities far exceed those found at the cellular level in metazoans. A unique feature is the almost universal separation of the nuclear material into two parts, a larger macronucleus and at least one micronucleus, with important differences in function. The genus *Paramecium* is representative, and its species have been the subject of many investigations.

The Paramecium: *General Structure.* If any forms can be called the omnipresent protozoans of fresh water, they are *Paramecium aurelia* and *P. caudatum*. No species of large size occur more commonly in cultures or under a wider range of conditions. Moreover, these species can be easily cultured in the laboratory and are favorable for study. The account to follow deals with *P. caudatum*, unless otherwise stated.

The size of the individuals seen in mixed cultures varies greatly. Like other kinds of animals which have been extensively studied, *P. caudatum* consists of many races which breed true among themselves but may differ widely when one race is compared with another. Reproduction, food, and environmental factors also influence body size. The cell is spindle-shaped, with the anterior end bluntly rounded and the posterior end more pointed (Fig. 8.17). At one side, a depression, the **oral groove**, passes diagonally from the anterior end to about the middle of the body, where it ends in a **gullet**. The body is covered with **cilia**, which are of uniform length except for those at the posterior end and in the oral groove, which are slightly longer. Within the gullet the cilia are arranged in a special band-like **undulating membrane**. On the surface of the cell just posterior to the end of the oral groove lies the **anal spot**, where egestion occurs.

The outermost layer of the cell is a thin, elastic **pellicle**, which under high magnification shows a geometric pattern (Fig. 8.18) related to the regular distribution of the cilia and **trichocysts** (Fig. 8.19). Beneath the pellicle is the **ectoplasm**, from which the cilia and trichocysts originate. The trichocysts, found also in many other ciliates, are structures of problematic function. In the paramecium they appear to serve as defensive organelles; when stimulated, they emit long threads. In other ciliates they aid in the capture of food.

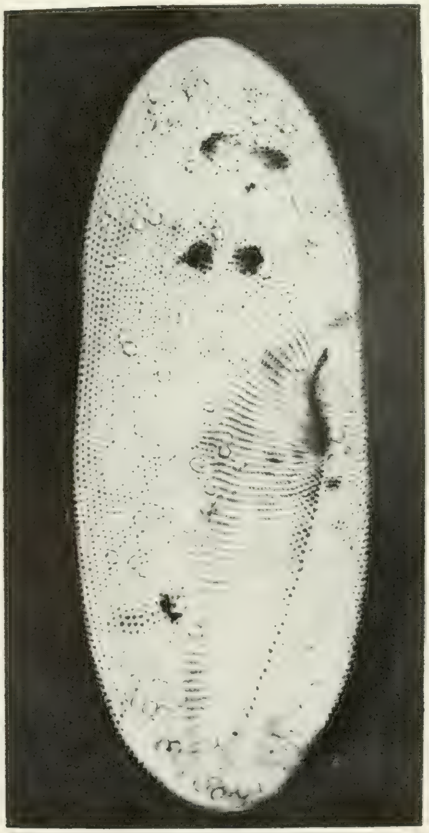


Fig. 8.18. *Paramecium:* structure of the pellicle. This is a photomicrograph of a special preparation which demonstrates the arrangement of the plate-like elements in the pellicle. These plates, and their relationships to cilia and trichocysts, are shown in greater detail in Figure 8.19. (Photograph courtesy General Biological Supply House, Inc.)

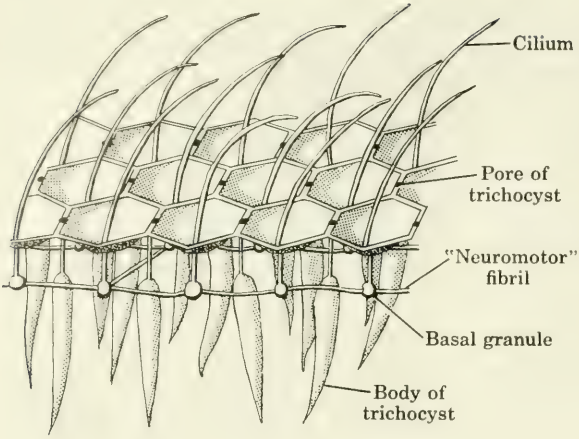


Fig. 8.19. *Paramecium:* relationship of pellicular structure to ectoplasmic organelles. (Adapted from E. E. Lund, 1935, University of California Publications in Zoology, vol. 39, printed by permission of the University of California Press.)

The greater part of the cell is composed of the **endoplasm**, which is sufficiently fluid to allow circulation of food vacuoles and other inclusions. The definite shape of the paramecium depends, therefore, on the relative rigidity of the ectoplasm and the pellicle. Within the endoplasm lies the **macronucleus**, related to the metabolic or vegetative activities of the cell, and the **micronucleus**, concerned with heredity and reproduction. *Paramecium aurelia* has two micronuclei, whereas *P. multimicronucleatum* has many. The endoplasm also contains two **contractile vacuoles**, one anterior and one posterior, and the **food vacuoles**. Larger masses of various sorts may also be found, in addition to the very small inclusions of the cytoplasm.

Movement and Responsiveness. Locomotion in *Paramecium* is effected by the action of the cilia, which by coordinated beating propel the animal in a spiral course. An understanding of this process involves two problems: first, that of explaining the operation of individual cilia; and second, that of accounting for the integration of the activities of the individual cilia in such a way as to provide for directed locomotion. The mechanism of ciliary action is not well understood, but it is clear that the physical state or configuration of the cilium must be altered between its "effective" stroke and its "recovery" stroke. It can be observed that the cilium is relatively stiff, and moves rapidly, during the effective or driving stroke, and that it becomes relatively limp and moves more slowly as it returns to its original position during the recovery phase (Fig. 8.20). The factors governing these changes presumably result from the interaction of the basal granule, or **kinetosome**, of the cilium and the **axial filament**, which springs from the kinetosome and runs the length of the cilium. Experiments have shown that a single cilium exhibits spontaneous movements as long as its connection with the kinetosome remains intact. Without the kinetosome, the cilium is incapable of beating. This indicates that a capacity for initiating activity resides in the kinetosome. It seems reasonable to speculate that a common physicochemical mechanism may underlie all phenomena of protoplasmic contractility, including amoeboid movement and ciliary and flagellary action, as well as muscular contraction.

Paramecium is propelled in its course by the beating of its thousands of cilia, but their beat is not random. Successive "metachronal" waves of action sweep smoothly along each row of cilia from the anterior to the posterior end of the animal, indicating that the ciliary beat is coordinated by some integrating activity. These waves can be interrupted by making transverse incisions through the ectoplasm of a paramecium; this demonstrates conclusively that the coordinating influences are conducted longitudinally through the ectoplasm. Looking for a structural foundation for these phenomena, we find that the kinetosomes of the cilia are interconnected in longitudinal rows by fibrillar strands, all of which are related to a central ectoplasmic structure near the mouth. It is difficult to avoid the conclusion that the coordination of beating in the rows of cilia is mediated through this fibrillar system, which has therefore been termed the **neuromotor apparatus**; the central structure from which the strands radiate is called the **motorium**.

One further aspect of ciliary action in *Paramecium* and other ciliates remains problematic. In the "avoiding reaction," to be discussed below, the animal stops and moves abruptly backward for a short distance. This does not, however, involve merely a reversal of the metachronal waves; rather, **all** the cilia immediately and simultaneously reverse their actions. Investigations of this phenomenon have yielded rather equivocal answers, but it appears certain that the reversal action is not mediated through the longitudinal ectoplasmic fibrillar system.

The locomotion of *Paramecium* is a composite of three basic movements: progression, rotation, and swerving. The animal moves forward, rotating on

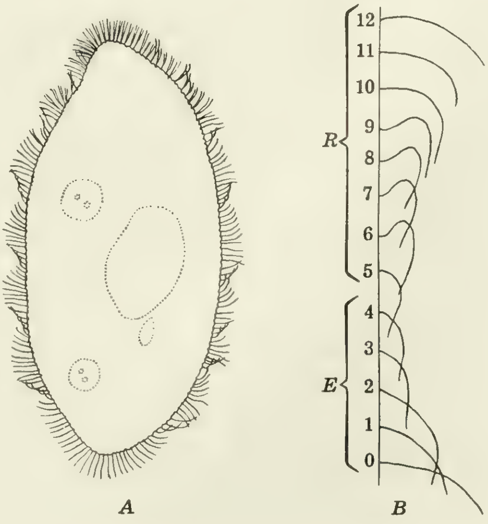


Fig. 8.20. Ciliary action. *A*, outline of a ciliate, showing metachronal waves of ciliary beat. *B*, phases of action of a single cilium; schematic. *E*, 0–4: successive stages in effective stroke; *R*, 5–12: stages in recovery phase. (Redrawn from K. von Frisch, 1952, *Biologie*, vol. 1, printed by permission of Bayerischer Schulbuch-Verlag.)

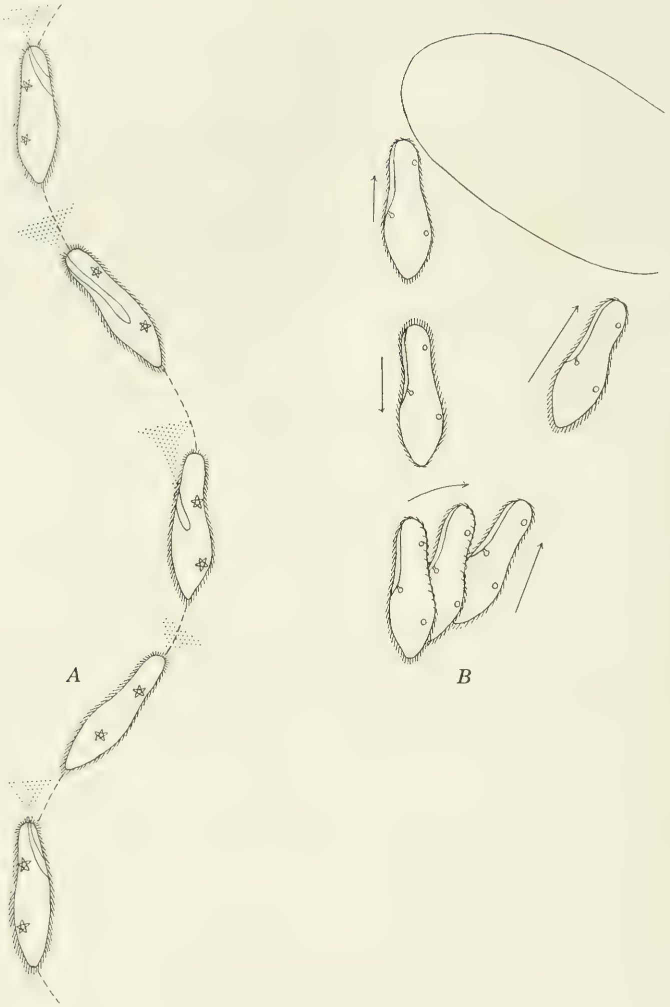


Fig. 8.21. *Paramecium:* locomotion, feeding, and the avoiding reaction. *A*, the spiral, rotating path described in swimming freely; the stippled cones represent the areas from which food particles are drawn into the oral groove. *B*, behavior of an individual encountering an obstacle; six successive positions. (Adapted from H. S. Jennings, *The Behavior of the Lower Organisms*, copyright 1906 by Columbia University Press, printed by permission.)

its long axis; an aboral swerving motion of the anterior end, in combination with progression and rotation, causes the animal to describe a spiral course instead of simply spinning like a rifle bullet (Fig. 8.21).

Paramecium generally reacts to stimuli by movement; therefore, variations of the locomotor patterns constitute its characteristic behavior. For example, its reaction to strong chemical stimulation involves swimming backward in a spiral for a considerable distance before resuming its forward progression. More commonly, in response to weaker chemical stimulation or to such a stimulus as contact with an obstacle, the animal exhibits a characteristic **avoiding reaction.** This involves stopping, reversing for a short distance, rolling in a cone-shaped path, and moving forward in a new direction. If this new path brings the animal again into contact with the obstacle, the pattern may be repeated indefinitely until the obstacle is cleared (Fig. 8.21). Such **trial-and-error** methods constitute a large proportion of the behavior of *Paramecium;* but by their infinite repetition, no matter how blindly, a suitable adjustment to environmental conditions can be effected. By thus demonstrating its ability to react to changes in its surroundings, the paramecium gives evidence of a capacity of **responsiveness** comparable with that found in other organisms.

In connection with the behavior of ciliates, the question arises whether these animals can learn from experience. There are accounts of what is claimed to be "learning," and reports of what appears to be the exercise of "choice" in the acceptance or rejection of food particles, among ciliates. To the extent that these reports are valid, the behavior of ciliates may be more complex than its usual trial-and-error features indicate.

Feeding and Metabolism. In feeding, the cilia of *Paramecium* draw a current of water against the oral surface, so that particles like bacteria, smaller protozoans, algae, and organic debris enter the gullet. By means of the cilia, and by movements of the gullet, masses of this food included in a drop of water pass into the cytoplasm and are thus **ingested.** The **food vacuoles** so formed move along a definite course within the cytosome carried passively by currents in a process termed **cyclosis.** As in *Amoeba*, it is assumed that enzymes are secreted into the vacuoles and bring about digestion. The products of digestion are evidently transferred into the surrounding endoplasm, since the vacuole finally contains only material to be **egested** at the **anal spot.** The observations which can be made on *Paramecium* are similar to those described for *Amoeba*, and we reason similarly from them with the aid of knowledge concerning other animals. The products of digestion, passing out of the food vacuoles, are utilized during metabolism. **Cellular respiration** corresponds to the process in vertebrates; oxygen enters the cell directly from the surrounding fluid, and final breakdown of the cellular constituents occurs, with transformation of energy and formation of waste products. **Excretion** of the wastes of metabolism occurs chiefly by diffusion over the entire surface of the cell and to some extent by means of the contractile vacuoles. Under suitable conditions the storage of reserves such as glycogen and fat occurs in the cytoplasm. The nutrition of *Paramecium* is, therefore, holozoic; and its metabolism is fundamentally like that of higher animals.

Life Cycle and Reproduction. The life cycle of *Paramecium* consists of an **active phase,** which may continue indefinitely in a suitable medium. There is no encysted phase that may be commonly observed in the laboratory, al-

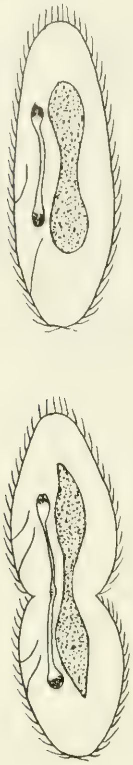
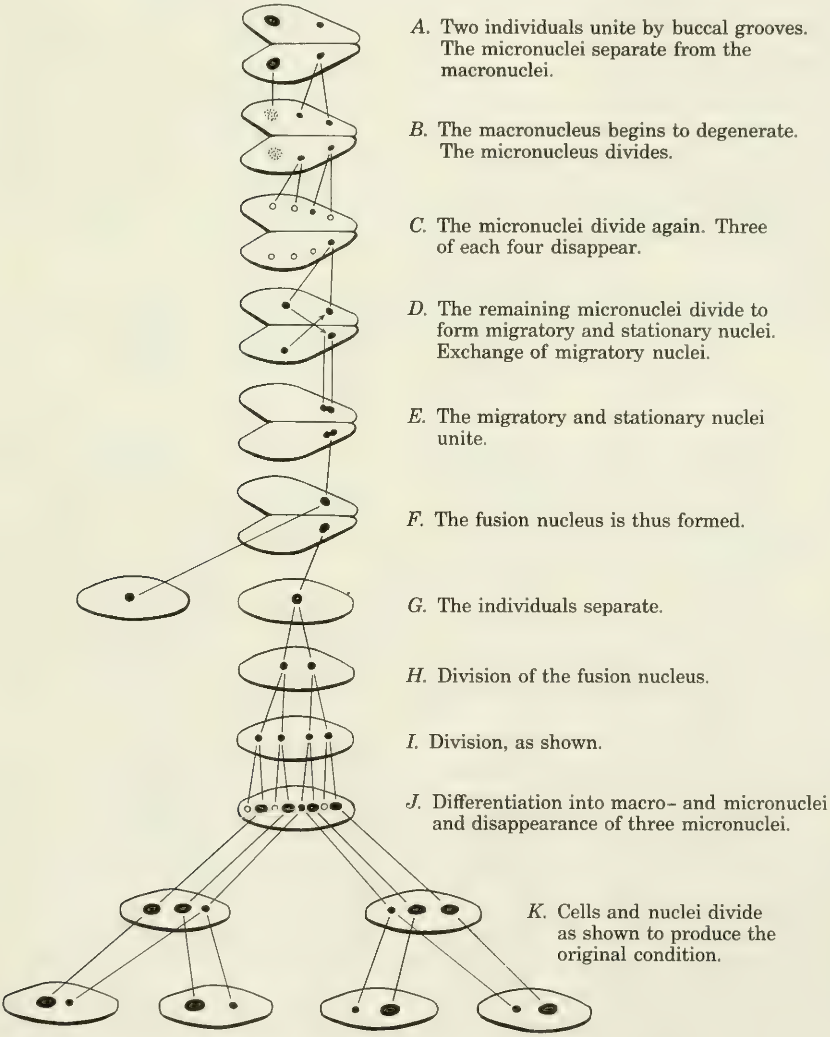


Fig. 8.22. *Paramecium:* binary fission. The macronucleus simply elongates and constricts, whereas the micronucleus divides by a mitotic process.

though encystment has been described. Perhaps it occurs more frequently in nature, since it is difficult to understand how any protozoan can be so universally distributed in fresh water without undergoing occasional encystment to survive periods of drought. *Paramecium,* however, does not appear to encyst upon aquatic vegetation; it is rarely, if ever, obtained by placing such vegetation in sterile water. In the laboratory the life cycle is an endless active phase with frequent reproduction by transverse binary fission, which is an asexual process. Periodic phases of nuclear reorganization, termed endomixis, also occur. Reproduction by conjugation, or temporary union of individuals with exchange of nuclear material, may also be observed. Some strains of *Paramecium,* however, appear capable of maintaining themselves indefinitely, by fission and endomixis, without conjugation.

In the course of **binary fission,** by which reproduction is accomplished, the macronucleus divides amitotically by elongation and constriction; the micronucleus undergoes a kind of mitosis (Fig. 8.22). As division of the two nuclei nears completion, the cell body becomes constricted and finally separates into two daughter cells of equal size. Meanwhile, one new contractile vacuole has been formed for each daughter, and a new gullet has arisen in each from the oral region of the parent cell. After separation the daughter cells usually grow to full size before the next division. Under favorable conditions there may be as many as 4 divisions, with the production of 16 individuals, in 24 hours. The rate of reproduction is determined by external conditions, such as food and temperature, and by internal factors.

Although *Paramecium aurelia* and probably other species of the same genus may live indefinitely without **conjugation**, this process apparently occurs under natural conditions as well as in the laboratory. In some cultures



A. Two individuals unite by buccal grooves. The micronuclei separate from the macronuclei.

B. The macronucleus begins to degenerate. The micronucleus divides.

C. The micronuclei divide again. Three of each four disappear.

D. The remaining micronuclei divide to form migratory and stationary nuclei. Exchange of migratory nuclei.

E. The migratory and stationary nuclei unite.

F. The fusion nucleus is thus formed.

G. The individuals separate.

H. Division of the fusion nucleus.

I. Division, as shown.

J. Differentiation into macro- and micronuclei and disappearance of three micronuclei.

K. Cells and nuclei divide as shown to produce the original condition.

Fig. 8.23. *Paramecium:* sequence of events in conjugation and subsequent divisions. (Adapted from H. S. Jennings, *Life and Death, Heredity and Evolution in Unicellular Organisms*, copyright 1920 by R. G. Badger, printed by permission of Chapman and Grimes, Inc.)

maintained for long periods (Calkins, *P. caudatum*), it was observed that conjugation occurred at intervals of some 200 generations. In others (Woodruff, *P. aurelia*), it was found that conjugation did not occur, even in many thousands of generations. The details of conjugation in *P. caudatum*, after the two individuals have fused together in the region of the buccal grooves, are shown in Figure 8.23, which should be carefully studied. The process differs remarkably from the syngamy, or permanent fusion of gametes, which occurs in many other protozoans as well as in higher animals. Syngamy involves the permanent and complete union of two cell bodies and their nuclei; conjugation consists of a temporary union and exchange of nuclear material, and it is known to occur only in the Ciliophora. However, the net outcome is the same in syngamy and in conjugation. The result of syngamy is a single cell with nuclear contributions from two cells. In conjugation, two cells unite temporarily, and after they separate, each "exconjugant" has a nucleus of double origin. Conjugation thus appears actually to be more efficient than syngamic fertilization, because the result of conjugation is two cells, each with a new combination of chromosomes. In fertilization the outcome is a single cell, the zygote.

In **endomixis** the macronucleus and a considerable portion of the micronuclear material disappear. From a single persistent micronucleus, new macro- and micronuclei are formed. Thus endomixis involves a nuclear reorganization comparable with that occurring during conjugation, but endomixis takes place within a single individual. Endomixis and binary fission are commonly regarded as **asexual** methods of reproduction; conjugation is considered a **sexual** process, although the two members of a conjugating pair are not obviously differentiated as male and female cells.

In 1937, within the species *Paramecium aurelia*, a number of "mating types" were discovered which are related to the occurrence of conjugation. In each of several morphological varieties of this species two mating types were recognized; individuals conjugate only with members of the opposite mating type within their own variety. Similar phenomena have since been described for other species of *Paramecium*, and for other ciliates as well. The existence of mating types may be taken as evidence of **physiological differentiation** between individuals, possibly related to the kind of differentiation which has led to the development of sexual dimorphism in other animals. The protozoan mating types, however, are not opposite sexes in the usual sense, as indicated by the fact that the transfer of nuclear material between the two individuals is mutual.

The full significance of conjugation in ciliates is still unsettled. It is clear that the resulting exconjugants are individuals with new chromosomal complements and new characteristics, as are the zygotes which result from fertilization in metazoans. The question that has led to endless investigation and discussion for years is whether conjugation has an important physiological effect upon what may be termed **cell vitality**, as measured by the rate of cell division; upon the longevity of the race; and upon normal cell activities.

Do these organisms grow old and die unless they are "rejuvenated" by conjugation? In some species such a rejuvenescence seems to occur, if the experimental evidence cannot be accounted for on other grounds. At the very least, conjugation, like other kinds of sexual reproduction, provides for a species the advantages of new nuclear combinations which make for greater variability and adaptiveness.

Other Ciliates. The class Ciliata includes most of the species of large Protozoa occurring commonly in fresh water; therefore, this class will be reviewed by listing its principal subdivisions and the names of representative genera; some of the forms listed are illustrated in Figure 8.24.

Class **Ciliata**

Subclass **Protociliata**—cilia of equal length covering entire cell; leaf-shaped or ellipsoidal in shape; no cytostome; parasitic in intestine of amphibians and fishes. *Opalina* and *Protoopalina*.

Subclass **Euciliata**—ciliation and shape of cell specialized as indicated in the several orders; typically free-living, but some species in each order parasitic.

- Order **Holotrichida**—cilia of approximately equal length and uniformly covering the cell in most species; with or without a cytostome; without a special adoral zone of cilia. *Amphileptus*, *Coleps*, *Colpoda*, *Didinium*, *Dileptus*, *Frontonia*, *Lacrymaria*, *Lionotus*, *Paramecium*, *Prorodon*, etc.
- Order **Heterotrichida**—cilia of cell surface small or reduced in numbers as compared with the specialized ciliation of the oral region. *Nyctotherus*, *Spirostomum*, *Stentor*, etc.

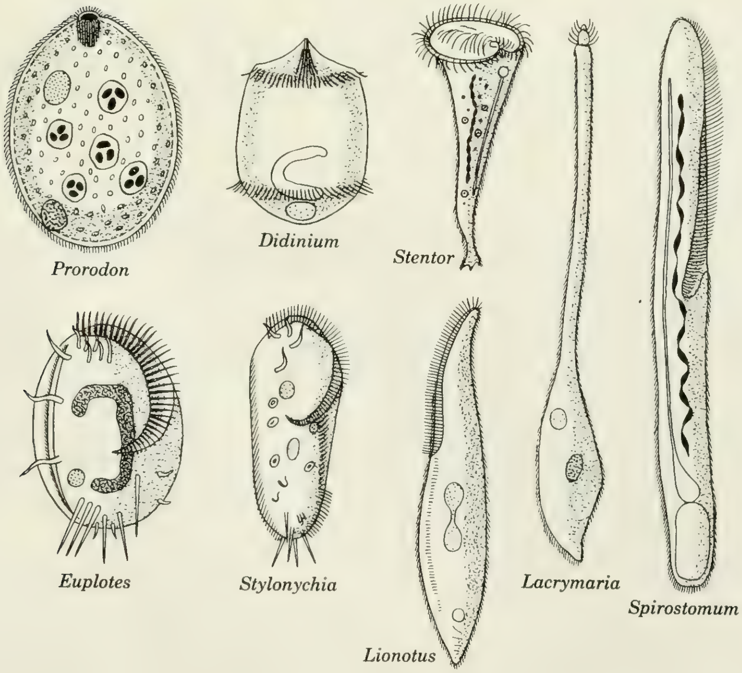


Fig. 8.24. Representative ciliates.

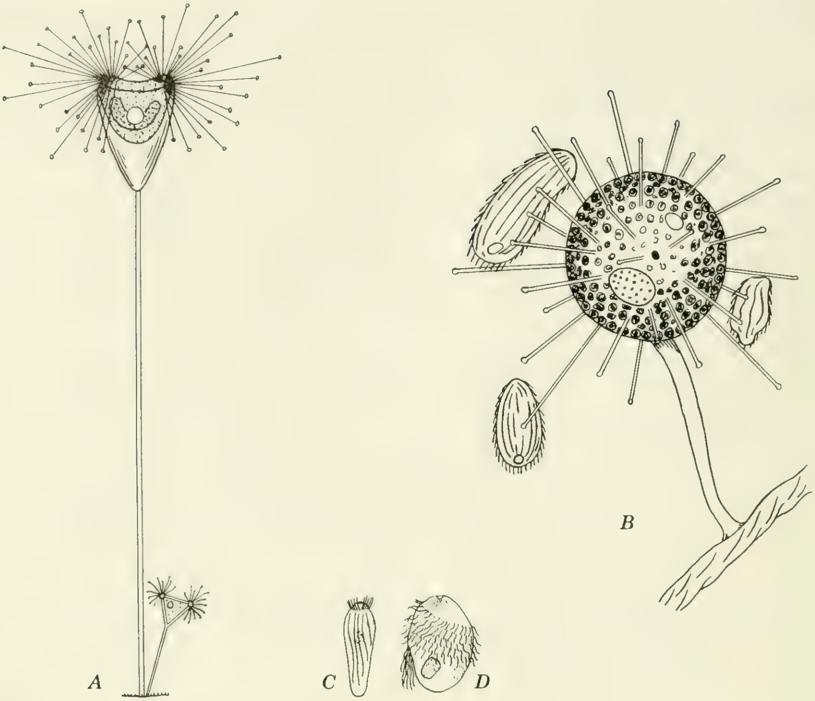


Fig. 8.25. Representative Suctoria, mature and immature stages. *A*, *Acineta; B*, *Podophrya*, feeding on small ciliates; *C*, ciliated juvenile stage of *Podophrya; D*, similar stage of *Tokophrya*. (*A*, adapted from W. S. Kent, 1880, *Manual of the Infusoria; C* and *D*, adapted, after A. Kahl, from R. P. Hall, *Protozoology*, copyright 1953 by Prentice-Hall, Inc., printed by permission.)

Order **Oligotrichida**—cilia greatly reduced in numbers and specialized; mostly parasitic and known principally from the digestive tracts of herbivorous mammals, but some free-living representatives. *Diplodinium*, *Halteria*, *Strombidium*, etc.

Order **Hypotrichida**—cilia scattered and highly specialized for locomotion and feeding; some as sensory organelles. Cell usually flattened and with what may be termed dorsal and ventral surfaces; typically creeping forms. *Euplotes*, *Stylonychia*, etc.

Order **Peritrichida**—cilia usually restricted to a conspicuous disc-like oral region and a basal region at opposite end; more familiar forms attached to substrate by a contractile stalk. *Carchesium*, *Epistylis*, *Trichodina*, *Vorticella*, *Zoothamnium*, etc.

The Suctoria

The class **Suctoria** comprises a small group of Protozoa placed in the subphylum Ciliophora because cilia are present during the immature, motile phase of the life cycle. During the adult, attached phase of the cycle the cilia are replaced by structures called tentacles, used in feeding. Representative genera are *Ephelota*, *Podophrya*, and others (Fig. 8.25). The mature animal is attached to the substratum by a stalk, and its tentacles radiate from the central cell body. Small organisms coming into contact with the knob-like ends of the tentacles are held fast. Apparently the tentacles digest their way through the surface of the captive. The fluid contents of the prey may be seen later streaming down through the tentacles into the body of the suctorian, as the prey, if it is small enough to be destroyed in this manner, slowly shrivels until released as a crumpled mass. Frequently a suctorian attacks ciliates much larger than itself, such as *Paramecium*, which is sometimes seen swimming with a *Podophrya* attached. Reproduction in suctorians involves cell division of a peculiar type which is usually termed **budding**. In this process the nuclei divide, as in *Paramecium*, one set of daughter nuclei being pinched off with a bud of cytoplasm into a temporary cavity within the distal end of the adult body. Within this cavity the bud gradually enlarges and develops bands of cilia. When it is released, it swims about by means of these cilia for a short time, then settles to the substrate and develops the stalk and tentacles of an adult. A process of conjugation is also known for the Suctoria.

Biogenesis

Historical. Some general problems intimately related to unicellular organisms may now be examined. One such problem involves the origin of living forms, or **biogenesis**. As a result of investigations extending over more than 200 years, it was shown during the third quarter of the nineteenth century that **abiogenesis**, or the spontaneous origin of organisms, does not occur. Organisms come from pre-existing organisms by the processes of reproduction. It was natural for the ancients to believe that animals such as insects, which suddenly swarmed in certain places, were produced from the mud of the fields under the influence of the sun's rays or arose spontaneously within the decomposing carcasses in which they were found. It was even supposed that mammals arose spontaneously within the female, although under the influence of seminal fluid from the male.

The higher animals were known to have parents, but the nature of the continuity between generations was not comprehended, except as the eggs of birds and reptiles produced young and mammals gave birth to living offspring. Gradually it was recognized that smaller animals also arise from eggs. The Italian naturalist, Redi, performed experiments (1688) which showed how maggots originate in meat from eggs laid by flies. He placed meat in jars, covering some with wire gauze and some with parchment and leaving others uncovered. Flies were attracted and laid their eggs upon the meat or upon the gauze. Maggots were seen to hatch from the eggs laid on the meat and to grow as they consumed the meat. The pupal stage and the emergence of the adult flies were observed. Maggots also hatched from eggs transferred from the gauze to the meat. The meat in the parchment-covered jars decomposed without the appearance of maggots. Redi made other observations on the development of insects and reached the conclusion that all spontaneous generation was presumably due to the introduction of living "germs" from without.

In 1676, the Hollander, Antony van Leeuwenhoek, discovered with the microscope, which had recently come into use as a scientific instrument, what he described as "little animals observed in rain, well, sea, and snow water as also in water wherein pepper had lain infused." Among other forms of life he observed some of the larger bacteria and many protozoans. During the eighteenth century the observations of Leeuwenhoek were extended by other workers until the important types of microscopic animals became known. Although larger organisms were seen to arise from eggs or seeds, it could still be believed that microorganisms arose spontaneously if conditions were suitable. This belief was not unnatural in view of the sudden appearance of these forms in the great numbers often observed in laboratory cultures. Some biologists from Redi onward, reasoning by analogy with higher organisms, believed that microorganisms arose from pre-existing forms. Others clung to belief in spontaneous generation. In spite of repeated failures to find evidence of abiogenesis, the question was reopened on theoretical grounds by Pouchet in 1859.

Final Establishment of Biogenesis. The work of Louis Pasteur (1822–1895) and his contemporaries, about 1860 1864, was stimulated by this reopening of the problem. A series of brilliant researches by this great Frenchman, by the German Koch (1843–1910), and by others finally showed that even the smallest organisms arise by division from parent forms. Species of protozoans and of bacteria were followed stage by stage until the life cycles of representative types were known in their active and in their resting phases. The English physicist, Tyndall, during investigations upon light about 1876, studied the "floating matter of the air" and showed that it teems with spores and other resistant stages of microorganisms which need only settle upon a proper medium to germinate. The English surgeon, Lister (1827–1912), and others who investigated the germ theory of disease as applied to surgery demonstrated that the germs found in wounds are not generated within the body but are introduced, as the spores or the active stages of such minute organisms may be introduced into a sterile culture medium. The extension of these demonstrations and of the Cell Theory completed the overthrow of abiogenesis and established biogenesis as the true explanation of the origin of new individuals. The saying of an earlier time, *omne vivum ex ovo*, every living thing from an egg, and a later one, *omnis cellula e cellula*, every cell from a cell, express the facts as now established.

The long controversy over biogenesis was related throughout its history to the observation that infectious diseases spread and multiply like living organisms. When it was discovered that organisms living as parasites are the causative agents in many such diseases, the basis for the observed facts became apparent. Still problematical, however, were the increasing number of infectious diseases in which no parasitic organisms could be discovered. In these cases it appeared that "something" was present which increased like an organism during growth; this entity came to be called a **virus.** A virus was shown to be something invisible, capable of passing through filters which retained bacteria. It was further discovered that although a virus could be transferred from cell to cell and continue its multiplication, it was unable to grow or multiply except in which it was found. Diseases now known to be caused by viruses include the type of sleeping sickness called encephalitis, as well as hog cholera, poliomyelitis, parrot fever, smallpox, yellow fever, and a long list of plant diseases, notably the

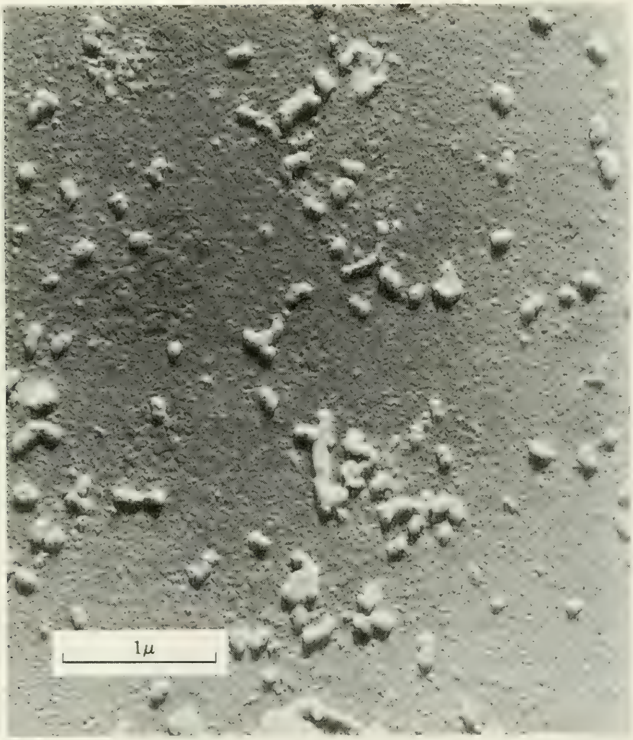


Fig. 8.26. The virus causing influenza in man. The particles are normally individual spherules, but in being prepared for this electron micrograph many have clumped together or have collapsed on the plastic film used to support the preparation. The line marked 1μ represents 1 micron (0.001 mm) enlarged to the same degree as the virus particles. (Electron micrograph courtesy D. E. Philpott.)

mosaic disease of tobacco. In addition, many types of viruses are known which attack the cells of bacteria; these are called "bacteriophages."

With the development of the electron microscope (see Fig. 2.4, p. 16), which makes possible the visualization of particles thousands of times smaller than the smallest ones visible with the light microscope, virus particles could be "seen" for the first time (Fig. 8.26). An individual particle has the general characteristics of a complex molecule, and viruses can be prepared as crystalline substances. In this "non-living," crystalline state they are infective for living cells of suitable hosts. Infection with a virus disease involves the introduction of a few particles into the cells of the host. These particles rapidly monopolize the metabolic processes of the host cell, shunting its synthetic mechanisms from the manufacture of the normal products of the cell to the duplication of virus nucleic acids and proteins. This, of course, profoundly affects the vitality of the host cell, and the symptoms of the disease are the direct or indirect results of such interference with cellular metabolism. Studies with bacteriophage have revealed that bacterial cells sensitive to the "phage" may be disrupted within a few hours, releasing thousands of new virus bodies. On the other hand, a virus particle entering an insensitive bacterial cell may remain quiescent, behaving more or less like a normal gene of the cell and being transmitted like a gene from one generation of the host to another.

The origin and possible relationships of viruses are unknown. By some, they are interpreted as modern representatives of an extremely primitive stage in the evolution of terrestrial life. If viruses are primitive, they may well represent a stage of life at which large, complex molecules of protein and nucleic acid first evolved the ability to metabolize in the presence of the proper substrate, and to organize the surrounding materials into duplicates of their own structure. According to this hypothesis, the metabolic requirements of viruses, once plentiful everywhere, can now be found in the proper combinations only within living cells. Viruses have been called "naked genes," and indeed their composition and activities, particularly the phenomenon of self-duplication, seem to be similar to those we associate with genes. All studies agree, however, in the conclusion that viruses contain no DNA (see p. 22); as in no other organisms known, the mechanisms of heredity in viruses appear to involve only proteins and RNA.

Alternatively, the viruses may be regarded as extremely degenerate forms of life, which in adaptation to parasitism have reached the ultimate in parasitic reduction. By this interpretation, viruses have become so specialized and so dependent upon conditions within host cells that when removed from this environment they revert to a "non-living," crystalline state. Whatever their true nature and history, viruses are clearly on the boundary line between living and non-living matter. The intensity of present research into the characteristics and properties of viruses is a measure of the potential value of these studies in terms of the conquest of disease, as well as of the increase in our knowledge of the vital processes of living things.

The Protozoan Cell

Returning to the Protozoa, we may conclude that the members of this phylum are single cells which exhibit the fundamental capacities of metabolism, responsiveness, and reproduction; they are, therefore, capable of going about the business of living as individuals which are single cells. Structurally speaking, an amoeba is an animal reduced to essentially the simplest terms.

It should be recalled that, alternatively, the Protozoa may be regarded as non-cellular animals, as animals whose bodies are not subdivided into cells. However, the bodies of protozoans exhibit fundamental similarities to the cells of other organisms, both in their basic structure and in their physiological activities. The question of the nature of protozoans is largely a philosophical one, but it seems reasonable to believe that both Protozoa and Metazoa arose by evolution from a common ancestry of single-celled forms. In their descent from such ancestry, the Protozoa have undergone specialization within the limits of a single cell, except insofar as species have arisen which consist of colonial aggregations of cells or individuals. These colonial forms will be discussed in the next chapter. The Metazoa, on the other hand, have specialized as many-celled individuals in which there is a division of labor between cells, and hence an unbalanced physiological state for the individual cell. There are species among the Protozoa whose cellular organization is far more complex than that of any metazoan cell, because specialization within the limits of the unicellular state is the unique direction in which the Protozoa have evolved. Yet the most complex of these protozoan cells can be regarded as single cells thus specialized and need not be considered as organisms having nothing in common with the cells of metazoans.

Unfortunately, there is no fossil record which shows, like the record of vertebrate evolution, how unicellular and multicellular animals arose, or from what ancestry they were derived. The record does show that protozoans such as the Radiolaria were in existence at the period represented by the oldest known rocks containing animal fossils, and that the Foraminifera are only a little younger as a group. From this fact it may be presumed that there were simpler protozoans aeons before that early period, because morphological simplicity must logically antedate such complexity as that of the shelled amoeboid forms. A one-celled animal, no matter how specialized it may become as a cell, is obviously simpler as an animal than a many-celled one. From this standpoint the Protozoa are the simplest of animals, and they seem to be more like the ancestors of all animal life than any other animals now in existence.

CHAPTER 9

MULTICELLULARITY, AND THE SIMPLEST METAZOAN ANIMALS:

Mesozoa and Porifera

In Chapter 8 we discussed representatives of the phylum Protozoa, modern descendants of the primitive one-celled animals; these have been limited in their specializations to the same one-celled plan of organization which must have characterized their remote ancestors. Earlier, it was pointed out that a significant epoch in the evolutionary history of animals was marked by the rise of forms consisting of many cells, each cell an integral unit playing its part in the economy of the individual, and in its special activities subservient to the whole complex. Without question, the evolution of multicellularity opened vast new potentialities and made possible the development of the Animal Kingdom as we know it. In view of the fundamental similarities demonstrated between the vital functions of Protozoa and those of higher animals, it appears most reasonable to assume that Protozoa and Metazoa had a common ancestry, and that the progenitors of both lines were one-celled organisms.

In this chapter we shall consider the manner in which many-celled animals may be thought to have arisen from these unicellular forebears, and some implications of the multicellular condition for the further progress of the Metazoa. In addition, we shall discuss briefly two of the modern phyla, the Mesozoa and the Porifera. These groups are so unlike the true Metazoa that they have been placed in separate branches, the Mesozoa and the Parazoa

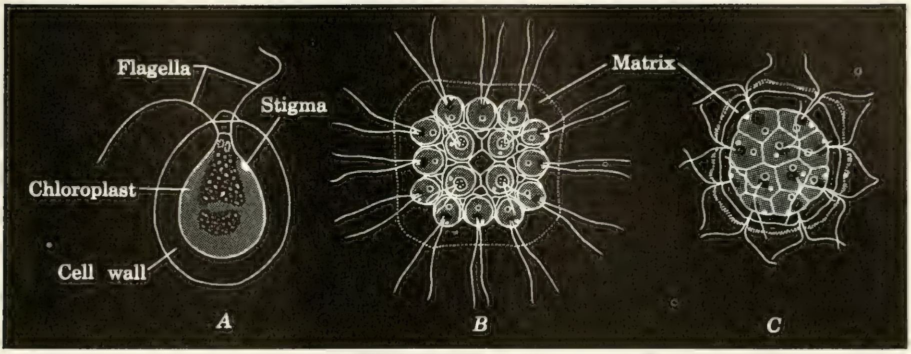


Fig. 9.1. Solitary and colonial plant-like flagellates. *A*, *Chlamydomonas*, a solitary individual. *B*, *Gonium pectorale*, a plate-like colony of 16 individuals. *C*, *Pandorina morum*, a solid, mulberry-like colony. (Adapted from G. M. Smith, *Fresh-water Algae of the United States*, first edition, copyright 1933 by McGraw-Hill Book Co., Inc., printed by permission.)

(see Fig. 7.4, p. 221). The simplicity of their organization, however, appears to present features which may have been characteristic of early metazoans.

Colonial Protozoa

Although the typical protozoan is a single cell, as we have seen, there are many species of Protozoa, particularly ciliates and flagellates, in which many similar cells live together in groups, or **colonies**, during a considerable part of the life cycle. The difference between these colonial protozoans and a metazoan lies in the relationship of the individual cell to the other cells with which it is associated. In the adult metazoan the cells can be classified as **somatic cells** and **germ cells**, depending on their relation to the reproductive process. This classification is not hard and fast; but in general the somatic cells are specialized for the various functions of metabolism and responsiveness, whereas the germ cells are specialized for **sexual reproduction**. During **asexual reproduction** in a metazoan, there may be formative cells which can be called reproductive insofar as they become an important source for the cells of the new parts. In asexual phases no cells that are comparable to the germ cells, with their strictly reproductive functions, may be present. Most important in the metazoan is the fact that the various kinds of somatic cells, as well as the germ cells, are dependent on the collective activities of the metazoan individual. The cell of a metazoan is a unit subordinated to the activities of the multicellular whole, which is the organism.

By contrast, the protozoan cell is an independent, self-sustaining individual. In most colonial protozoans, each cell of the colony is likewise an independent individual, so far as the fundamental capacities of metabolism, responsiveness, and reproduction are concerned. In such a species the colony eventually disintegrates by separation of its units, so that each cell goes its way, encysting, dividing, conjugating, or uniting with another cell in syngamy, until a new colony is formed again from a single cell by repeated divisions and by the remaining together of the daughter cells. Every cell of the colony is, therefore, as independent functionally as though there were no colonial stage in the life cycle. Such species are manifestly no more than aggregations of independent protozoan cells, each of which is sufficient unto itself, or **physiologically balanced.**

In a few species of colonial Protozoa, however, the distinction can be made between somatic cells, which are destined to die, and germ cells, which can in a sense continue to live by contributing their substance to the next generation, if they become gametes and unite in syngamy. A comparison of these species with other Protozoa, on the one hand, and with the Metazoa, on the other, makes clear the basic continuity in reproductive processes from one end of the Animal Kingdom to the other. Such a comparison also indicates that this primitive step in differentiation may have been fundamental in leading to the development of truly multicellular types, with their characteristic wide additional specializations within the somatic cell line.

A series of forms in the flagellate family **Volvocidae** will be used for this discussion, although this family belongs among the Phytomastigina or plant-like flagellates. Of course, no inference is intended that this series of forms marks the actual pathway of the development of multicellularity in animals. Rather, this alignment represents merely an arrangement of existing organisms into a series showing an increase in **mutual interdependence** between the individuals of the colony. The many-celled condition in animals may well have arisen through some analogous process.

The members of the family Volvocidae are colonial forms of varying size and complexity, the colonies in each species consisting of a specific number of component individuals. These individuals strongly resemble a simple, non-colonial flagellate of the genus *Chlamydomonas* (Fig. 9.1), which is covered by a cell wall of cellulose, bears two flagella, and contains a prominent chloroplast, a sensitive pigmented eye spot, and two contractile vacuoles. A simple colonial form of the genus *Gonium* may be composed of 4 of these units, or of 16, depending on the species. In *Gonium*, the individuals are arranged in a flat plate, and as in all the Volvocidae the colony is held together by a mucilaginous **matrix** secreted by the individuals. Aside from the fact that the colony moves as a unit, propelled by the flagella which all lie on one side of the plate, the cells are independent in their functions, and hence each is physiologically balanced. This is indicated by their behavior in reproduction: asexually, each of the cells may divide repeatedly to form a small daughter colony, and these then separate and grow to the size of the parent colony. Sexual reproduction is brought about when the individuals of the colony separate as **isogametes** (gametes without differences in size) and unite in pairs to form zygotes. From the zygotes new daughter colonies arise by cell division, without separation of the daughter cells.

Pandorina colonies consist of 8, 16, or 32 individual cells resembling *Chlamydomonas*, arranged in an oval mass (Fig. 9.1). Reproduction may be asexual, as in *Gonium*, when each individual divides repeatedly to form a daughter colony. Sexual reproduction also occurs, involving either the fusion of isogametes (**isogamy**) or syngamy between different-sized gametes (**anisogametes**); a transition to **anisogamy** is indicated here.

Eudorina is a colony of 8, 16, 32, or even 64 individuals (Fig. 9.2). Reproduction occurs as in *Pandorina*, except that in sexual reproduction anisogamy is the rule, the two kinds of gametes being produced consistently in different colonies.

Pleodorina, sometimes considered a variety of *Eudorina*, exists in two forms showing interesting differences. Whereas in the colonial species just described, all the cells of the colony are capable of reproduction, in *Pleodorina illinoisensis* a group of 4 individuals at one pole of the spherical, 32-cell colony are smaller and are incapable either of asexual reproduction or of forming gametes (Fig. 9.2). Only 28 of the cells may thus be said to retain the physiological balance characteristic of all the cells in a *Pandorina* colony, for example. In another species, *Pleodorina californica*, only half the 64 or 128 cells retain the ability to reproduce; the other half have become, in effect, **somatic cells**.

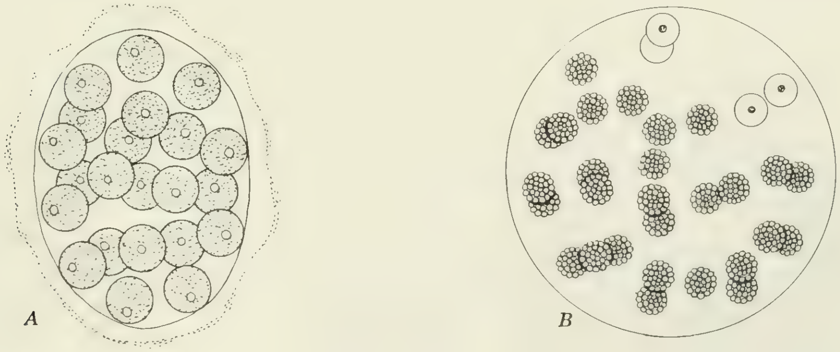


Fig. 9.2. Further development of colonial plant-like flagellates. *A*, *Eudorina elegans*, a hollow, ovoid colony of flagellated individuals; the flagella have been omitted from this figure. *B*, *Pleodorina illinoisensis*, in asexual reproduction. The 4 "somatic cells," or sterile individuals, remain undivided, whereas each of the other 28 individuals ("germ cells") produces a daughter colony.

Volvox itself stands at the apex of this series. A colony of *V. globator*, typical of the genus, consists of some hundreds or thousands of cells, arranged in a single layer about the periphery of a hollow ball (Fig. 9.3). Each of the individuals composing the colony lies in a polygonal segment of the common matrix. In favorable preparations, each can be seen to be interconnected with its neighbors by delicate protoplasmic bridges. These interconnections presumably mediate coordinating influences which enable the relatively huge colony to progress through the water in a directed fashion. They also make possible the maintenance of a measure of integration of the activities of the component individuals. Reproduction in *Volvox* is a function of only a relatively few individuals, which either enlarge and sink into the central cavity to produce daughter colonies by repeated asexual divisions or similarly enlarge and transform into either eggs or sperm bundles. Syngamy between these anisogametes results in the formation of a zygote which secretes about itself a heavy cyst wall and is thus enabled to survive conditions which result in the death of the parent colony. The significant feature of *Volvox* is the fact that, as in the Metazoa, only a relatively few cells retain the power of reproduction and can be termed **germ cells**. The vast majority of the component cells are concerned not with the maintenance of the species through reproduction but only with the maintenance of the individual (or colony) through their metabolic activities. Such a loss of physiological balance on the part of the somatic cells is characteristic of the Metazoa; it is thus possible to regard *Volvox*, and in the same sense *Pleodorina*, as multicellular organisms rather than as colonies of protozoan cells.

From our accounts of the Protozoa in the preceding chapter, it is clear that there are no gross discontinuities between the vital functions of Protozoa and those of Metazoa, aside from the fact that the protozoans carry on all their activities within the confines of a single cell. Consideration of the series of colonial protozoans just described emphasizes the fact that the development of colonial organization in at least one group of modern Protozoa has progressed to the point at which, in effect, multicellularity has been attained. Thus it appears that the capacity of developing multicellularity is not lacking in protozoans. We may conclude that through some similar persistence of aggregations of one-celled animals, with the gradual emergence of the characteristics of an **integrated organism** from the collective activities of its component, originally independent units, a point was reached making possible the rise of more complex many-celled animals. As previously indicated, the next step involved in this progression, after the differentiation of somatic and germinal cells, is the further specialization of somatic cells into specific structural and functional types, each capable of performing with added efficiency one or a few special functions.

The two phyla now to be considered, the Mesozoa and the Porifera, represent the simplest metazoan types known to exist. In these it will be seen that the specialization of somatic cell types, and the division of labor among them, has progressed to a considerable degree. Unfortunately, in the absence of

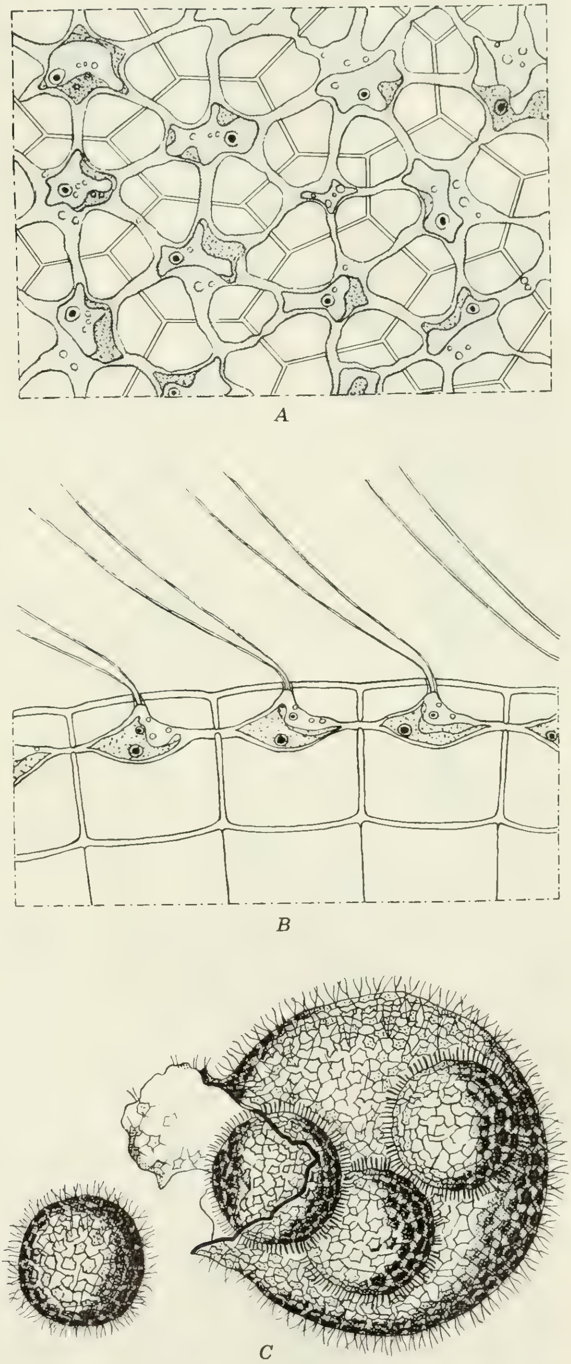


Fig. 9.3. *Volvox aureus: A*, surface view of a portion of the colony; *B*, sectional view of the edge of a colony; *C*, parent colony rupturing, releasing young daughter colonies. (*A* and *B*, after C. Janet, 1912, *Le Volvox; C*, adapted from K. von Frisch, 1952, *Biologie*, vol. 1, printed by permission of Bayerischer Schulbuch-Verlag.)

types intermediate between highly organized colonial Protozoa and these simple Metazoa, we must bridge the evolutionary gap with logical conjecture, reasoning from the known facts to supply the missing information.

The Phylum Mesozoa

All Mesozoa are parasites within the bodies of other animals. They may be defined as animals consisting of an outer syncytial or cellular layer, commonly ciliated, which encloses one or more cells giving rise to the gametes and to another type of reproductive cells called **agametes.** The life cycle is complicated and apparently includes asexual and sexual generations, which alternate. The phylum includes the single class **Moruloidea,** which contains the order **Dicyemida** and the order **Orthonectida.** The members of this phylum are the simplest of all the truly many-celled animals. This simplicity, however, is perhaps an outcome of degeneration, since all Mesozoa are parasitic during the greater part of their life cycles. Parasites commonly show structural simplification, as compared with their free-living relatives, and the Mesozoa may have degenerated greatly in the course of their evolution. Such modification may have gone so far that it would be impossible to identify the free-living type from which the Mesozoa have evolved, even if this type were still in existence. Many zoologists regard the Mesozoa as greatly degenerated flatworms, but there is no clear evidence for an evolutionary origin of this sort. The Mesozoa constitute a small but well-defined group, important because its members possess a simpler organization than that of any other group of many-celled animals. They can, therefore, be taken at their face value as the simplest metazoans of the present day, even though they may have arisen from more complex ancestors and become simplified as a result of their parasitic existence.

Structure and Life Cycle. The dicyemids, as members of the Dicyemida are called, occur as parasites in the excretory organs (nephridia) of squids and octopi. They are small, elongate animals, a few millimeters in length, consisting of very few cells, often a total of less than 25 (Fig. 9.4). An outer layer of these cells, ciliated, encloses an inner **axial cell** or cells from which the **reproductive cells** arise. The outer or **somatic cells** are differentiated into a **head region** and a **trunk region.** The structure of a dicyemid is thus extremely simple, but the life cycle is complex and is not known completely for any single species. Apparently, from the single axial cell, many cells are formed which are called **agametes** because, although they are not ova, they develop without fertilization. This is an instance, rare among Metazoa, in which a single cell, which is a germinal cell but not a gamete, is capable of producing the new generation. Development of the agametes gives rise to numbers of asexually reproducing individuals, the **nematogens.** Eventually, a new type of individual, the **rhombogen,** appears and produces still another form, the **infusorigen.** Remaining within its parent rhombogen, the in-

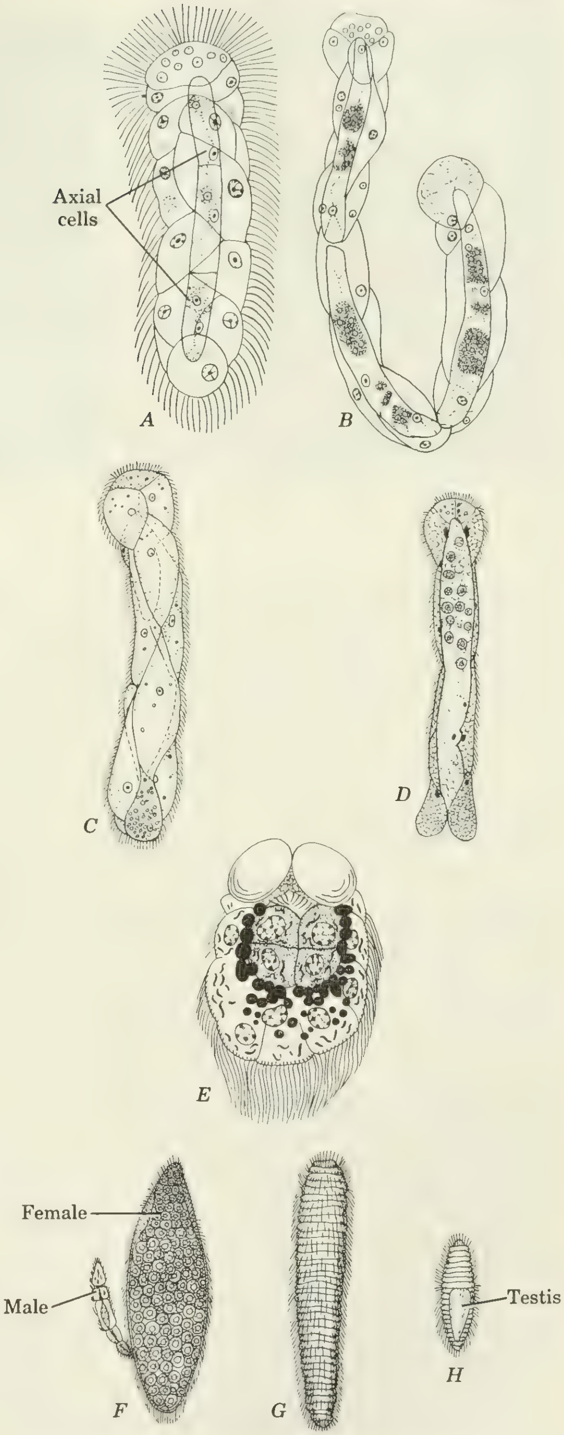


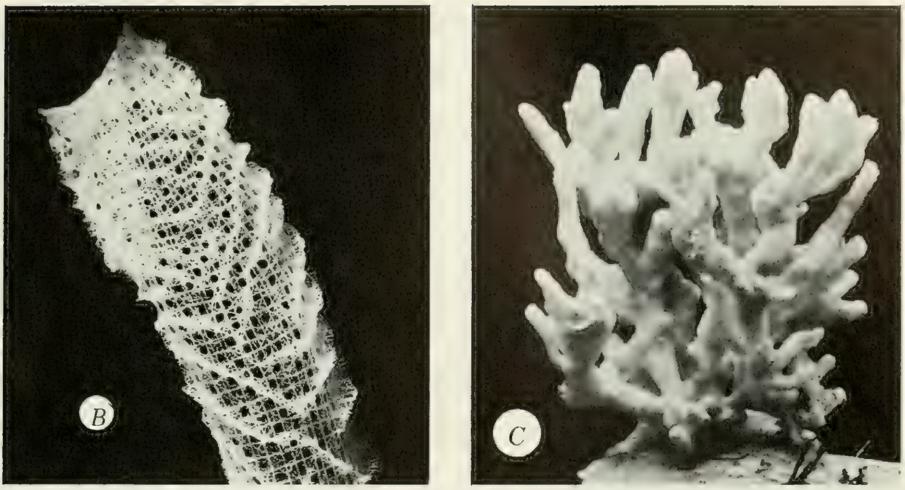
Fig. 9.4. Mesozoans. *A* through *E* are selected stages in the life cycle of Dicyemida, occurring in the excretory organs of cephalopod mollusks. *F* through *H* are sexually reproductive phases of various Orthonectida. *A*, immature dicyemid in a very young squid. *B*, later stage, containing masses of cells developing from agametes to produce **nematogens.** *C*, nematogen. *D*, nematogen in optical section, showing the internal cells which give rise to further generations of nematogens, or to other stages known as **rhombogens** and **infusorigens.** *E*, ciliated **infusoriform** larva which leaves the host. Beyond this point the life cycle is unknown. *F*, fertilization in an orthonectid. *G*, mature female, and *H*, mature male. The larval stages of these forms are masses of cells (plasmodia) occurring in a variety of invertebrate hosts. (Redrawn, after various authors, from L. H. Hyman, *The Invertebrates; Protozoa through Ctenophora*, copyright 1940 by McGraw-Hill Book Co., Inc., printed by permission.)

Fig. 9.5. Types of sponges. *A*, Calcarea: *Scypha*, three living individuals. *B*, Hexactinellida: portion of the skeleton of a glass sponge, *Euplectella*. *C*, Monaxonida: *Microciona*. (*A* and *C*, photographs by George Lower; *B*, photograph by Bassett Maguire, Jr.)

fusorigen develops male and female gametes. These unite in syngamy, and the divisions of the zygotes thus formed give rise to numerous **infusoriform larvae**. The larvae are liberated from the body of the parent (and grandparent) and leave the host, but their further history is completely mysterious. They survive only brief periods in sea water and are apparently incapable of infecting squids and octopi. It thus appears that an unknown intermediate host must be involved in the cycle but, despite the efforts of many competent investigators, further information is unavailable.

In the Orthonectida, the life cycle also includes parasitic asexual phases; these are more or less structureless, multinucleate masses of protoplasm inhabiting a variety of invertebrate hosts. In addition, free-living males and females are known which produce sperm and egg cells. These cells are released into the sea and unite in syngamy to form zygotes, which develop into ciliated larvae resembling those of dicyemids. The larvae are infective for the invertebrate hosts, and, having gained entry, transform into the asexual form (Fig. 9.4).

The Body Plan and Life Cycle. To generalize, the mesozoan body consists of a small number of body cells, surrounding a parent germ cell capable of producing many agametes. The agametes are single cells, each of which can reproduce a new individual. In some and perhaps all species gametes are eventually produced, so that there is an irregular alternation of sexual and asexual generations. Although the mesozoan is hardly more complicated than some colonial protozoans, it is clearly a metazoan animal. Even if its simplicity has resulted secondarily from a parasitic mode of life, it is an example of a very lowly type of metazoan. If its simplicity is really primitive, the mesozoan type is very important because it suggests a possible step in the evolution of many-celled from single-celled animals.



A significant difference in the organization of the Mesozoa as compared with that of the more advanced Eumetazoa is the nature of the inner cell layer. Only in the Mesozoa is the inner cell mass exclusively reproductive; in higher Metazoa the inner cells are concerned with nutrition.

The Phylum Porifera

Porifera are the simplest multicellular animals constituting a well-defined group which includes a considerable number of species. They may be characterized as Metazoa with tissues of a very simple sort but without organs; with a more or less extensive system of internal cavities but without a digestive cavity or enteron; and usually with an internal skeleton. The name Porifera ("pore bearers") is derived from the many small openings upon the exposed surface, through which water enters on its way to the internal cavities, and the fewer large openings through which this water is expelled. The phylum **Porifera** includes three classes (Figs. 9.5 and 9.6): the class **Calcarea**, in which the skeleton is calcareous and in which are grouped the simplest sponges, such as *Leucosolenia* and *Scypha;* the class **Hexactinellida**, with skeletons of glass; and the class **Demospongiae**, in which are included the natural fibrous bath sponges and related forms. In general the skeletons of sponges are composed of minute spicules, of proteinaceous fibers as in the bath sponge, or of both spicules and fibers. The spicules of sponges are often of such characteristic shapes that families and even genera may be identified by spicules alone. These spicules, like the skeletons of Radiolaria and Foraminifera (p. 236), occur in the debris upon the bottom of the ocean and are often found in sedimentary rocks. Fragments of sponges, as well as isolated masses

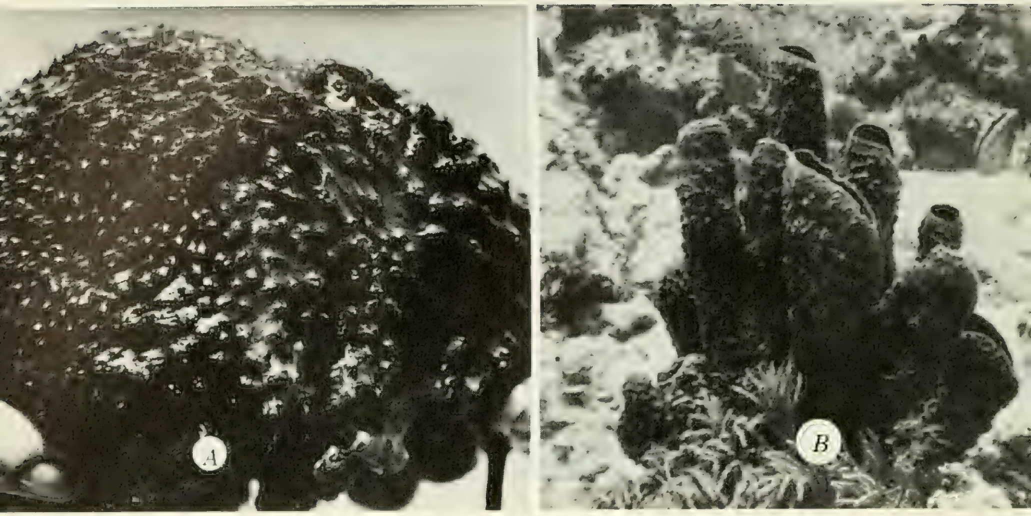


Fig. 9.6. Types of sponges, continued: Keratosa. *A*, living bath sponge, *Spongia*. *B*, a horny sponge, *Hircinia*, in its natural coral reef habitat. (Photographs by John F. Storr.)

of spicules, occur as fossils in Pre-Cambrian and later deposits; the evolutionary history of sponges thus covers more than half a billion years, and no group of animals has a longer fossil record.

All sponges are marine, except for a very few fresh-water forms, and most occur in shallow water. They are typically firmly attached to the substrate at maturity, but there is a free-swimming, flagellated larva in the early developmental stages. Because of their attachment and manner of growth, sponges were first classified as plants. Later, because of their possession of flagellated cells with collars, they were regarded as protozoan colonies. They were later grouped with the Coelenterata, and it was not until the beginning of the present century that they were finally given their current taxonomic position as members of a unique and aberrant phylum.

The most familiar example of a sponge is *Spongia*, the fibrous skeleton of which is the natural bath sponge of commerce. A sponge of this type may be regarded as a colony of individuals, although the boundaries of these individuals are indefinite. To understand the organization of sponges, we must begin with forms much simpler than *Spongia*.

General Structure. ***The Olynthus.*** The structure of sponges is best explained by first describing the fundamental type from which all sponges have probably arisen in the evolutionary history of the phylum. This type, which is called the **olynthus**, was originally considered an adult sponge and was given the generic name *Olynthus*. It is now known to be a late stage in the development of certain species. An olynthus (Fig. 9.7) is a cylindrical organism, attached at its basal end, with an opening, the **osculum**, at its free end and an inner cavity known as the **spongocoel**. The walls of this hollow cylinder are perforated by incurrent **pores** (Fig. 9.8); these are intracellular canals passing through the cytoplasm of cells called **porocytes**. The external surface, and the distal surface of the spongocoel just within the osculum, are covered by a **dermal epithelium** of flattened cells. The remainder of the spongocoel is lined by a single layer of flagellated cells called **choanocytes** because of a protoplasmic collar surrounding the base of the flagellum on each cell. Between the dermal cells and the choanocyte layer is a middle region containing the **spicules**, with the cells that secrete them, the **scleroblasts**, and connective-tissue cells (Fig. 9.9). Wandering cells called **amoebocytes** are most numerous in this middle region, but they may occur in any part of the body. These migrate by amoeboid movements like the white blood cells of a vertebrate. The **archaeocytes**, a large type of amoebocyte, are also found

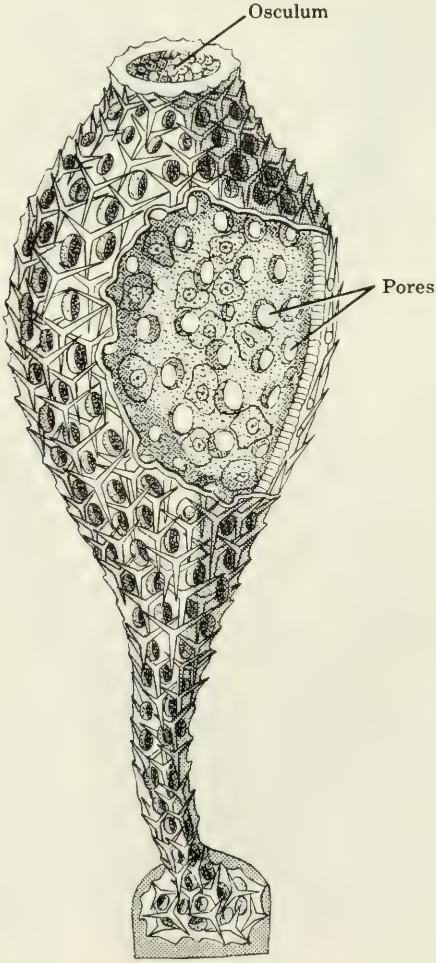


Fig. 9.7. Olynthus stage of a calcareous sponge; diagrammatic. (Redrawn from E. Haeckel, 1872, *Die Kalkschwämme*.)

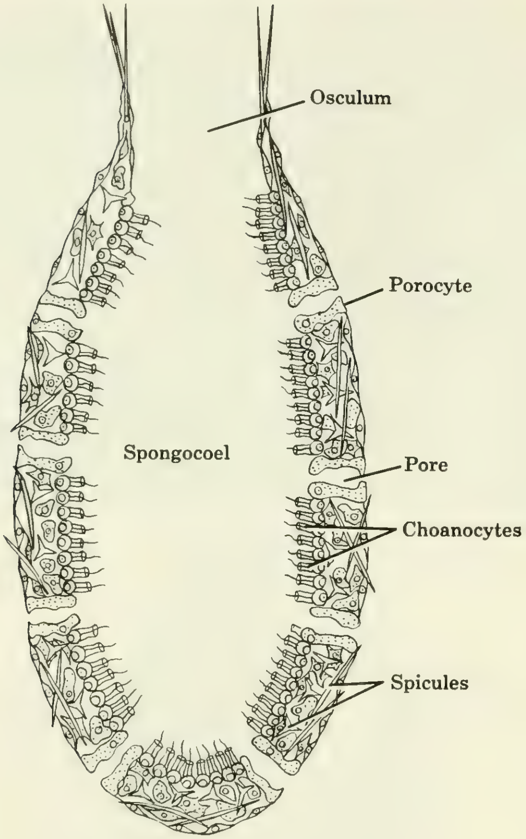


Fig. 9.8. Diagrammatic longitudinal section of an asconoid sponge. (Adapted from L. H. Hyman, *The Invertebrates: Protozoa through Ctenophora*, copyright 1940 by McGraw-Hill Book Co., Inc., printed by permission.)

here. These are considered totipotent cells and have been described as capable of differentiating into all the other cell types, including gametes.

More Complex Sponges. The simplest adult sponges, such as *Leucosolenia*, arise by budding and growth from an olynthus. More complex sponges are modified in a great variety of ways, but their units of organization, the canal systems, can be derived from a type like the olynthus. A series of these modifications is shown diagrammatically in Figure 9.10. The primary type of canal system found in the olynthus is termed the **asconoid** type. A second type, called **syconoid**, found in such sponges as *Scypha*, is actually derived in development by the folding of the wall of an olynthus stage and subsequent differentiation. Additional cavities are thus formed within the sponge, and the course of water from the exterior to the osculum becomes more complicated. The openings in the surface of *Scypha* are not the same as the pores of the olynthus, which correspond rather to those leading from the so-called **incurrent canals** to the **excurrent canals**. In the adult *Scypha* these pores are no longer intracellular channels; the porocytes of the olynthus stage disappear during development. Other changes involve the restriction of the choanocytes to the linings of the excurrent canals and the extension of the dermal epithelium to line the entire spongocoel. The homologies between the asconoid and syconoid types are clear, however. The third, or **leuconoid**, type of canal system can be derived by folding of the wall of the syconoid type with its two sets of canals, and by the development of extensive **subdermal spaces** within which water circulates on its way to the flagellated chambers. The most highly organized sponges have very elaborate canal systems and small, spherical flagellated chambers, but all can be compared, in the manner indicated, with the simple arrangement in the asconoid type. These higher sponges are further complicated by increase in the number of oscula and spongocoels, each the center of a canal system, and by the indefinite growth of the entire mass.

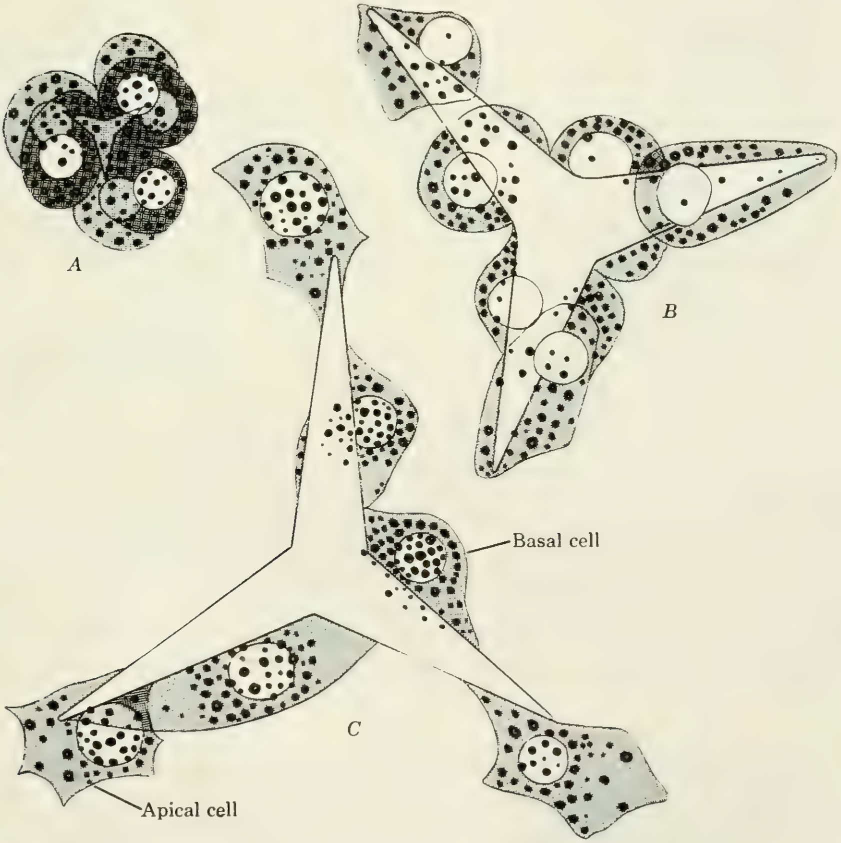


Fig. 9.9. Stages in the formation of a triradiate spicule by scleroblasts in a calcareous sponge. Individual cells come together to form a "trio"; each cell then divides, and the resulting "sextet" (*A*) forms and finishes the spicule (*B* and *C*). Among the cells of the sextet, basal and apical cells may usually be distinguished. (Adapted from E. A. Minchin, 1898, *Quarterly Journal of Microscopical Science*, vol. 40.)

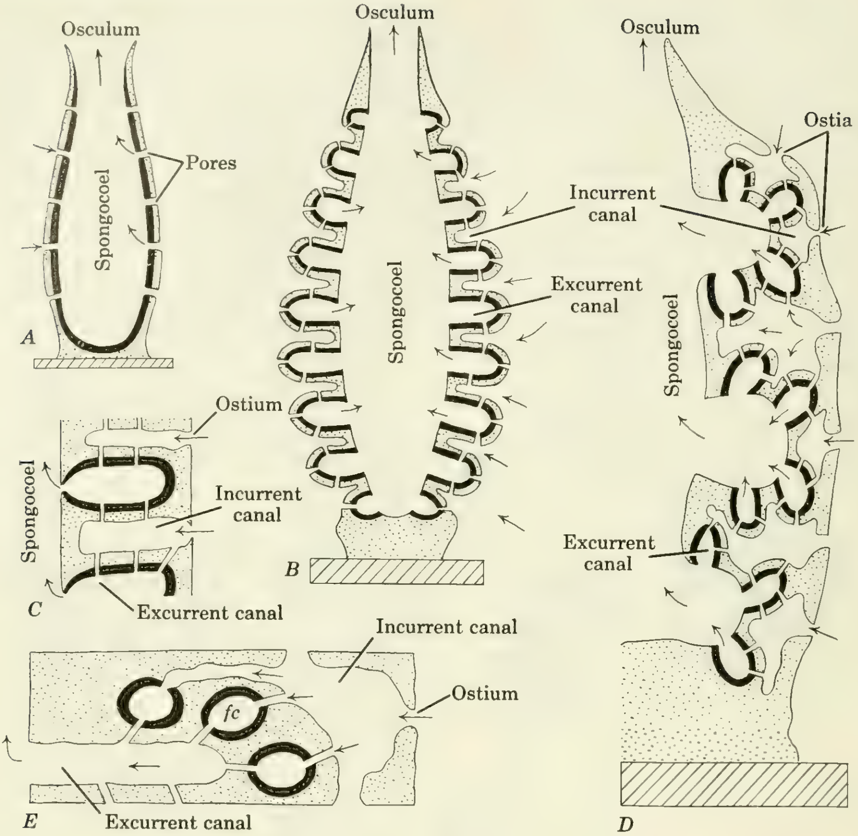

Osculum
Pores
Spongocoel
A
Osculum
Spongocoel
B
Osculum
Ostia
Incurrent canal
Excurrent canal
Spongocoel
Excurrent canal
D
Ostium
Spongocoel
Incurrent canal
C
Excurrent canal
Incurrent canal
Ostium
fc
E
Excurrent canal

Fig. 9.10. Comparison of various types of sponge structure; diagrammatic. The dark areas represent choanocyte layers; arrows indicate direction of water currents. *A*, asconoid type, with spongocoel completely lined by choanocytes. *B*, simple syconoid type, with choanocytes in excurrent canals only. *C*, more complex syconoid type, with thickened walls and narrowed openings into incurrent canals. *D*, primitive leuconoid type, with excurrent canals in groups opening into branches of the spongocoel. *E*, more advanced leuconoid type; the choanocytes are restricted to small, spherical flagellated chambers (*fc*) which are considerably removed from both the outer surface and the spongocoel. (Redrawn with modifications from E. A. Minchin, in Lankester's *Treatise on Zoology*, 1900.)

Few sponges are symmetrical like *Leucosolenia* and *Scypha*, although the radial symmetry of these genera and of the olynthus appears to be the primitive state from which all sponges have been derived in the evolution of the phylum. Moreover, there may be great differences in shape among the individuals of the species, for the growth of a sponge is much influenced by conditions in the immediate environment.

Metabolism. The food of sponges consists of microorganisms and particles of organic detritus which enter the canal systems with the inflowing water and are ingested by the choanocytes, which are also responsible for maintaining the water currents. In view of the rapid growth of many sponges, the nutrition is evidently very effective. The metabolism of sponges, which because of the structure of these animals is difficult to study, is assumed to be similar to that of other animals in which it is better understood.

When a sponge is exposed to a suspension of carbon particles (India ink) or carmine granules in sea water, some of the particles enter the surface openings with the currents of water. Later, when bits of the sponge are examined, the granules are found within certain of the cells, just as such particles are seen after ingestion by a paramecium (Fig. 9.11). Unicellular organisms have been observed undergoing ingestion in a similar manner in sponges. Digestion is undoubtedly intracellular, as in Protozoa. In the calcareous sponge *Scypha*, the food particles are ingested chiefly by the choanocytes and are then passed into nearby amoebocytes. Since the amoebocytes are migratory and are capable of differentiating into other cell types, the food may thus be distributed to all parts of the sponge. Storage of reserves, carbohydrates and fats, occurs in modified amoebocytes. Excretory processes occur at the cellular level, and soluble excreta and carbon dioxide are readily removed by the currents of water passing through the canal system. An abundant supply of oxygen for respiration is provided by the same water currents.

Responsiveness. The flow of water into the minute openings upon the surface, through the canal systems and flagellated chambers to the spongocoel, and out the osculum is the factor that conditions all other activities of the sponge. This flow is maintained by the flagella of the choanocytes. The steady and strong currents so produced, and the directed nature of the currents, have been found to depend on rather precise adjustments of the relative diameters of incurrent and excurrent pores and canals. In sponges, the only easily demonstrable reactions to stimuli are the closing of pores and oscula and contractions of entire masses of cells, which may temporarily obliterate the canal systems. It is to be supposed that less violent reactions to various stimuli involve slight constriction or expansion of pores and canals, to bring about physiological adjustments of the volume and velocity of water flow. The presence of special contractile cells surrounding water passages has long been recognized (Fig. 9.12), but these were thought to operate as **independent effectors**, responding directly to stimulation without the inter-

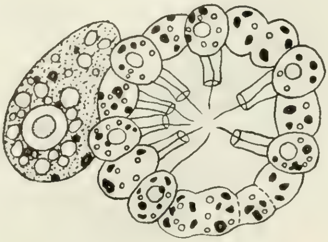


Fig. 9.11. Transfer of ingested particles from choanocytes to an amoebocyte. (Redrawn, after N. Pourbaix, from L. H. Hyman, *The Invertebrates: Protozoa through Ctenophora*, copyright 1940 by McGraw-Hill Book Co., Inc., printed by permission.)

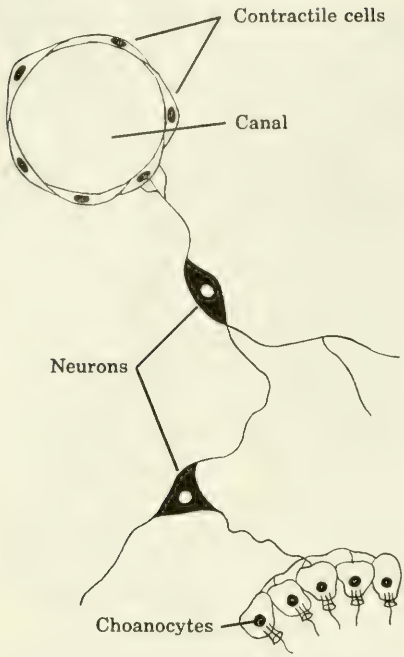


Fig. 9.12. Mechanisms of reception, conduction, and response in a calcareous sponge. Stimulation of choanocytes sets up nerve impulses which are conducted through a nerve net to effectors, such as contractile cells surrounding a canal. (Adapted from O. Tuzet, R. Loubatieres, and M. Pavans de Ceccatty, 1952, *Comptes rendus de l'académie des sciences*, vol. 234.)

vention of specialized nervous elements. Recently, students of sponges have demonstrated that a primitive type of nervous system does exist, in a wide variety of different types of sponges. This system appears to consist basically of a diffuse network of typical neurons, with processes connecting the choanocytes with contractile cells surrounding parts of the canal systems (Fig. 9.12). In addition some sponges possess large and highly specialized nerve cells which are lodged singly in vacuoles within the mesenchyme, and others which appear from their structure and connections to function as neurosensory cells. These new facts make it clear that coordination and responsiveness in sponges depend on the activities of cells specialized for reception of stimuli and conduction of impulses; presumably their functions are similar to those of the more highly developed nervous systems of more advanced animals. The reactions of sponges are limited and sluggish but are adequate for the needs of sponges, which are all either attached or incapable of locomotion as adults.

Reproduction and Development. Most sponges appear to be **monoecious** ("one house"), or hermaphroditic, and thus are capable of producing both male and female gametes. The eggs and sperms are frequently produced at different times in a single individual, however, making self-fertilization impossible. In **sexual reproduction** the **zygote** develops within the parent into a **flagellated larva** which is discharged through the osculum with the outgoing water. After a brief period of free life, the larva becomes attached and undergoes a peculiar type of development, in the course of which the flagellated external cells move to the interior and produce the choanocytes which line the spongocoel or the flagellated chambers (Fig. 9.13). In simpler forms, the olynthus stage is passed through; in more complex sponges, development may be more direct. The final stages may include much budding and growth, often leading to the formation of a large mass. This budding is comparable with the asexual reproduction occurring in other multicellular animals, although it is often difficult to distinguish from the general process of growth. The fresh-water sponges, and some marine forms, produce internal buds, termed **gemmules,** which are covered with resistant membranes and can survive severe conditions such as freezing and drying. In various other sponges, under adverse conditions, so-called **reduction bodies** are formed. These consist of masses of amoebocytes surrounded by dermal cells. They are less resistant than gemmules, but they serve a similar purpose in preserving the species through periods during which normal life would be impossible. With the return of favorable conditions, the gemmules or the reduction bodies can produce fully developed individuals.

Regeneration and Reassociation. Regeneration, by which lost parts are restored and even whole individuals are formed from small pieces, is commonly associated with conspicuous powers of asexual reproduction. The extensive budding and vegetative growth of which sponges are capable would lead us to expect greater powers of regeneration than seem to exist in these animals. Some sponges will regenerate from cuttings, and artificial propagation of commercially valuable sponges has been attempted, without marked success, by planting small cuttings in favorable locations.

In at least a few types of sponges there is a remarkable capacity of reassociation of cells after the organization of the body has been completely disrupted. For example, pieces of *Microciona prolifera*, the common red

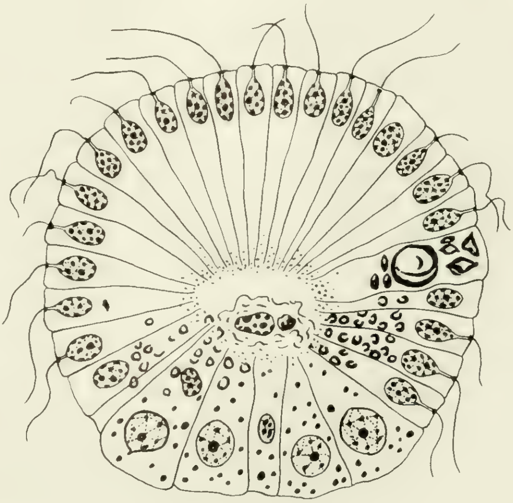


Fig. 9.13. Flagellated **amphiblastula** larva of a calcareous sponge, *Grantia compressa*. The developing sponge reaches this stage before it is released from the parent. After a brief free-swimming period, it settles to the substratum and transforms into the sessile adult form. (Redrawn from O. Duboscq and O. Tuzet, 1937, *Archives de zoologie expérimentale et générale*, vol. 79.)

sponge of the Atlantic coast, can be squeezed through silk bolting cloth of very fine mesh, so that the cells of the sponge are almost completely separated or dissociated. If these dissociated cells are allowed to settle upon the bottom of a dish of sea water and remain undisturbed, they immediately begin to coalesce into small multicellular masses. These masses continue to fuse, forming thin encrustations over the substratum, and under favorable conditions large sponges like the original will eventually be formed. The phenomenon of reassociation involves very interesting problems. It demonstrates with remarkable clarity the relatively loose organization characteristic of the sponge body; what is particularly remarkable is the fact that the capacity of reforming their original organization resides in isolated cells. A similar ability to reassociate occurs to a limited extent in some simple coelenterates, and such phenomena can be demonstrated in embryonic stages of more highly specialized animals (p. 167).

The loose association of cells in the sponge body, together with the relatively slight degree of specialization exhibited by the somatic cells of sponges, is a cogent reason for considering sponges to be at the **cellular** level of organization, in contrast with the unicellular protozoans and the tissue-grade organisms of more advanced phyla.

The Sponge Body Plan

To speak of the sponge body raises the question of what constitutes the individual in animals of this phylum. In the olynthus, or in such a sponge as *Scypha*, an individual with a single osculum is recognizable. In other sponges, which grow into large masses with many oscula, the entire mass may be called an individual; or, the individual may be defined as any part of the entire mass that includes an osculum and its related canal system. However we define the individual sponge, the body plan basic for the phylum is the one seen in the olynthus stage and in its simpler derivatives. In the cellular organization of the sponge body, there are tissues of a simple kind but no organs. The early stages of development are peculiar, and it is difficult to reconcile the layers of the sponge body with the embryonic germ layers of more complex animals. Finally, the sponge has no internal cavity homologous with the digestive cavity or enteron of higher animals. This last feature of bodily structure, together with the primitive cellular organization and the peculiar mode of development, gives the phylum its unique position among the Metazoa.

Evolutionary Significance of Mesozoa and Porifera

The fact that both Mesozoa and Porifera are multicellular organisms and show some cellular differentiation warrants placing them among the Metazoa.

However, their peculiarities of organization and their simplicity clearly indicate that, phylogenetically, they antedate all other members of this subkingdom. (In this statement we are assuming that the Mesozoa are primarily simple, and not secondarily simplified organisms.) Both may be assumed to have arisen from somewhere near the point of origin of multicellular animals from unicellular ancestors, and the history of both groups, particularly of the sponges, is marked by a certain amount of evolutionary progress. This progress has advanced in different directions in the two groups, but in neither has the path led in the direction taken by more progressive animals. No metazoans other than Mesozoa, for example, possess as their only internal tissue a cell mass specialized exclusively for reproduction; none but the sponges has as its only internal cavity a system of water chambers lined by choanocytes.

It therefore seems reasonable to conclude that the three simplest metazoan phyla, Mesozoa, Porifera, and Coelenterata (which will be discussed in the next chapter), represent groups which evolved independently, and at different times, from primitive multicellular ancestors. Of the three fundamental body plans characteristic of these groups, those of the Mesozoa and Porifera were evidently so limited in evolutionary possibilities that only the modern representatives of these same phyla can be traced to them. The basic coelenterate plan, with an internal digestive tissue later excavated to form a hollow enteron, was apparently sufficiently adaptable to the needs of animals to serve as the basis for further evolution.

CHAPTER **10**

RADIAL ANIMALS:
The Phyla Coelenterata and Ctenophora

The phyla **Coelenterata** and **Ctenophora** contain the relatively simple types of animals characterized by radial to biradial symmetry and by a generally primitive plan of organization. This plan centers about a single internal digestive cavity, typically with a single opening to the exterior. The bodies of these animals are frequently composed of only two cellular layers—one covering the external surface, the other lining the digestive cavity. Cellular differentiation has given rise to tissues, but the organs that are present are very primitive. Although the coelenterates and ctenophores are sometimes considered as subphyla within a single phylum Coelenterata, their fundamental differences justify placing them in separate phyla.

The Phylum Coelenterata

The Coelenterata are the simplest many-celled animals possessing the digestive cavity characteristic of all Metazoa except mesozoans and sponges. The digestive cavity with its single opening, the mouth-anus, is responsible for the name Coelenterata, literally "hollow intestine." Coelenterates may be defined as radially symmetrical animals consisting in the simplest cases of two layers of cells, **epidermis** and **gastrodermis**, separated by a non-living, non-cellular, secreted **supporting lamella**. This is true only of the most primitive forms; all others have developed a middle layer which contains cells and is therefore comparable with the mesenchyme, of mesodermal origin, in higher animals. Although this third layer is rudimentary at best, its presence casts doubt on the common general statement that coelenterates as a group are

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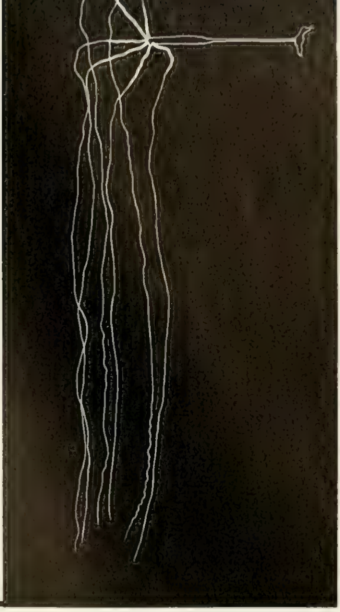


Fig. 10.1. *Pelmatohydra oligactis* in its normal attitude, attached to a submerged leaf, with tentacles extended. Note the attenuated, stalk-like basal portion of the trunk. (Redrawn from L. H. Hyman, 1930, *Transactions of the American Microscopical Society*, vol. 49.)

diploblastic. The typical radial symmetry has in some cases become biradial, with two centers of symmetry rather than one. Coelenterates are always provided with stinging capsules, the **nematocysts**, structures which are not known to be produced by any other animal group. The organs which occur in this phylum are simple in structure and function. As compared with sponges, coelenterates exhibit more definite form and symmetry and a more advanced level of organization.

The phylum includes three classes: the class **Hydrozoa**, containing the hydras, hydroids, hydromedusae or hydroid jellyfishes, and hydroid corals; the class **Scyphomedusae**, including jelly-fishes of a more advanced type; and the class **Anthozoa**, the sea anemones, sea pens, sea fans, and true stony corals.

Coelenterates are predominantly marine animals, occurring at all depths in the ocean and under a wide range of conditions, since the phylum contains both attached and free-swimming forms. Typically, however, they are inhabitants of the shallow waters along shore and of the upper layers of the deeper ocean. In their feeding habits they are strictly carnivorous, capturing other animals by means of tentacles armed with nematocysts, from which paralyzing threads are emitted. Most coelenterates are attached for a considerable part of the life cycle, during which they commonly reproduce by budding, and colonies of innumerable individuals may be produced. In Hydrozoa a free-swimming sexual phase may alternate with the attached, asexual stage; in Scyphomedusae the free-swimming jellyfish stage constitutes the major part of the life cycle; but in Anthozoa both asexual and sexual reproduction occurs during the attached phase, for no free-swimming reproductive individuals are produced. The radial symmetry characteristic of coelenterates is presumably related to the attached growth habit, since radial symmetry is commonly associated with a fixed mode of life or indicates descent from attached ancestors.

The fixed growth habit, together with the radial symmetry, led early naturalists to classify the coelenterates as plants. Their animal nature became apparent to zoologists in the eighteenth century when it was recognized that the organisms have mouths, tentacles, and digestive cavities. However, Aristotle's view that they were intermediate between plants and animals persisted until well into the nineteenth century and is reflected by the inclusion of the coelenterates, with the echinoderms, in a group called Radiata or Zoophyta ("animal-plants"). Only when it became clear that the structural organization of coelenterates is vastly simpler and more primitive than that of echinoderms was the modern phylum Coelenterata finally established.

Remains of coelenterates such as hydroids and corals appear in some of the earliest fossil-bearing rocks. Even jellyfishes have left a fossil record as thin, delicate carbon-film impressions in ancient sedimentary beds. Thus, the early evolution of coelenterates long antedates the beginning of our fossil record, and we have no direct information about their antecedents. Phylogenetic speculation must be based on the facts of development and probable interrelationships deduced from the life cycles of modern representatives.

Although they are by no means "typical" hydrozoans, the fresh-water hydras, long studied by zoologists, are widely distributed, easily obtainable, and relatively simple representatives of the phylum. They are also representative of the metazoans higher than sponges, for they have a digestive cavity and cell layers comparable with these features of the more advanced animals. Because of its relative simplicity, the hydra is particularly well suited to illustrate the structure of a metazoan. Accordingly, we shall examine the hydra as a coelenterate, but more especially as a simple metazoan, to be compared in structure and function with the vertebrate and with the protozoan.

THE CLASS HYDROZOA

The Hydra: ***Habitat and Activities.*** Several species of the genus *Hydra* occur in the United States. Related hydras are placed in different genera because of special characteristics. A common brown form, with very long tentacles and with its trunk region differentiated into a slender basal stalk and a stouter body, has been designated *Pelmatohydra oligactis* (Fig. 10.1). A green hydra, deriving its distinctive color from the presence of alga-like zoochlorellae in cells lining its digestive cavity, is recognized as *Chlorohydra viridissima.* Unless specific exceptions are noted, the following account is applicable in general to any type of hydra.

The individual hydra is usually found attached by its base to submerged objects, with its body extended. It may float freely, however; in an aquarium it is often seen attached to the surface film, hanging down into the water. Although there are no special organs of locomotion, the animal shifts its position by simple movements of the body or by a slow gliding of the base without detachment from the substratum. Hydras react positively to light of moderate intensity and so tend to collect in the lighted portion of an aquarium. This reaction is especially noticeable in the green hydra. But let us defer further consideration of habits and general behavior until the structures involved have been described.

General Structure. The body of a hydra consists of a simple two-layered tube (Fig. 10.2), the **trunk**, normally attached at one end, the **base**, and surmounted at the other by a circle of **tentacles**, varying in number. The tentacles enclose a conical region, the **hypostome**, which bears at its apex the **mouth**. The body wall surrounds a digestive cavity or **coelenteron**, which extends into the tentacles. The cell layers, an outer **epidermis** and an inner **gastrodermis**, are separated from each other by a non-cellular **supporting lamella**. This structure corresponds functionally to an elastic skeleton. It serves as a place of attachment for the cells and gives support and elasticity

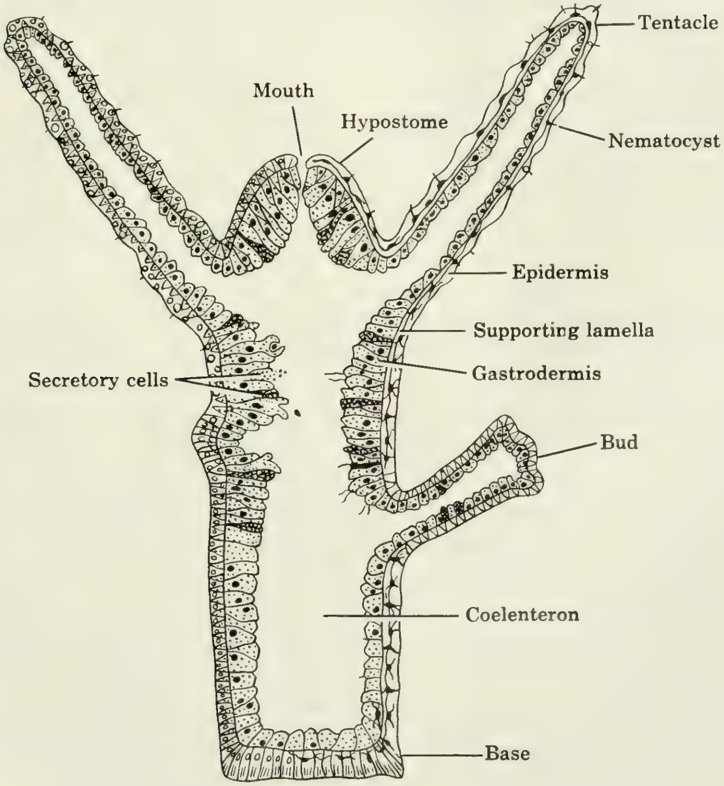


Fig. 10.2. *Hydra:* general structure, shown by a diagrammatic longitudinal section of the body.

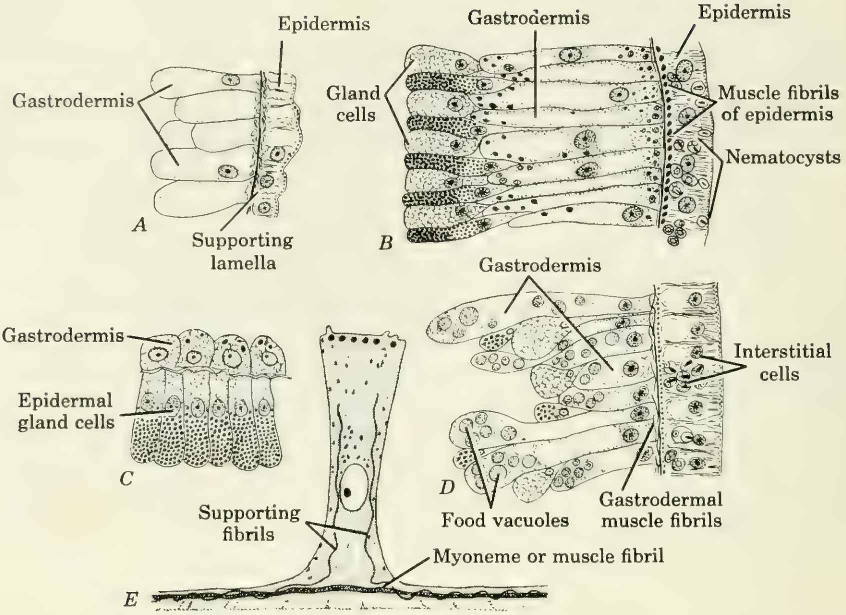

Epidermis
Gastrodermis
A
Supporting lamella
Gastrodermis
Epidermis
Gland cells
Muscle fibrils of epidermis
Nematocysts
B
Gastrodermis
Gastrodermis
Epidermal gland cells
C
Interstitial cells
D
Food vacuoles
Gastrodermal muscle fibrils
Supporting fibrils
Myoneme or muscle fibril
E

Fig. 10.3. Details of cellular structure in the hydra, as shown by cross sections through different regions of the body. *A*, in the stalk region, with very vacuolated gastrodermal cells. *B*, through the hypostome, showing glandular gastrodermal cells. *C*, through the pedal disk, with glandular epidermal cells. *D*, through the "stomach" region, showing digestive gland cells and food vacuoles. *E*, detail of a large epidermal epitheliomuscular cell. (*A–D*, redrawn from L. H. Hyman, *The Invertebrates: Protozoa through Ctenophora*, copyright 1940 by McGraw-Hill Book Co., Inc., printed by permission; *E*, after J. von Gelei.)

to the entire organism. In hydrozoan medusae, or jellyfish, this layer is represented by a thick, watery jelly without cells, termed the **mesogloea** ("middle-jelly").

Cellular Structure and Function. The outer cell layer, or **epidermis**, is composed principally of large **epitheliomuscular** cells (Fig. 10.3). These are so called because, in addition to their epithelial function of covering a surface, they also serve the function of contractility and make possible the movements of the animal. Each cell possesses contractile processes extending along the supporting lamella. In the epidermis, the contractile processes run lengthwise of the body tube, so that their coordinated contraction produces a shortening of the body. The corresponding muscle processes of similar cells in the gastrodermal layer extend along the circumference of the tube, at right angles to the epidermal processes, and their contraction lengthens the body by decreasing its diameter. The many changes of shape and position exhibited by the hydra are all produced by the coordinated and localized contractions of this simple muscular system. At the base of the body the epidermal cells are represented by glandular cells. These produce the secretion by which the attachment of the animal is effected. Interspersed between the large epidermal cells of the body and tentacles are numerous small **interstitial cells** and cells called **cnidoblasts** ("thread formers"), derived from interstitial cells. The **sensory cells** and **nerve cells** of the epidermis will be described in the discussion of responsiveness in the hydra.

The cnidoblasts, containing the **nematocysts** with which the hydra subdues its prey, are scattered throughout the epidermis but are most abundant upon the tentacles. Nematocysts are one of the most remarkable mechanisms in the Animal Kingdom. They are not cells, but non-living cell products, which might be likened to harpoons, ready to be shot from guns and capable of paralyzing any minute animal which they may strike. The presence of nematocysts is one of the distinguishing characteristics of all coelenterates. The bodies of these animals are soft and defenseless, except as some may withdraw within a protective skeleton; but the members of this phylum must be recognized as powerful enemies of the many small animals upon which they prey. The nematocysts of most coelenterates are not harmful to man, although those of some species may be irritating. The poison of a few species can induce a violent reaction of the human skin, serious general symptoms, and even death in sensitive individuals.

In the development of a nematocyst, an interstitial cell produces in its cytoplasm a minute structure resembling a vacuole; the early stages are so minute that the details of development are not well understood. However, the vacuole is later seen to be a capsule containing a fluid and a thread. The commonly accepted theory is that the thread, hollow in its final form, arises as an ingrowth from one end of the capsule. Clearly, the nematocyst is not a cell but a capsule containing an inverted thread, which is produced and retained until discharge within the cytoplasm of its cnidoblast, a modified interstitial cell. The discharge of a mature nematocyst involves the forceful eversion of the thread, like the turning right-side-out of an inturned glove finger. The sudden entrance of water into the capsule, possibly as a result of some rapid change in osmotic relations or in the permeability of a limiting membrane, is the most plausible explanation of this reaction. The greatly increased internal pressure thus forces the thread out.

Cnidoblasts may undergo differentiation from interstitial cells in parts of the body remote from the tentacles, in which nematocysts are most commonly used. In this case the cnidoblast is transferred over a considerable distance, coming to rest eventually in the epidermis of the tentacle. Here it becomes oriented with its trigger-like projection, the **cnidocil,** protruding from the general surface of the epithelium. The cnidocil is apparently the part of the cnidoblast most sensitive to external stimulation.

Because of the absence of nervous connections, the cnidoblasts are considered to be **independent effectors,** structures responding directly to stimuli and lacking nervous control. Nematocysts are little affected by purely mechanical stimuli, such as those produced by rubbing the tentacle with a clean glass rod or with a bit of clean blotting paper. Contact with a saliva-coated

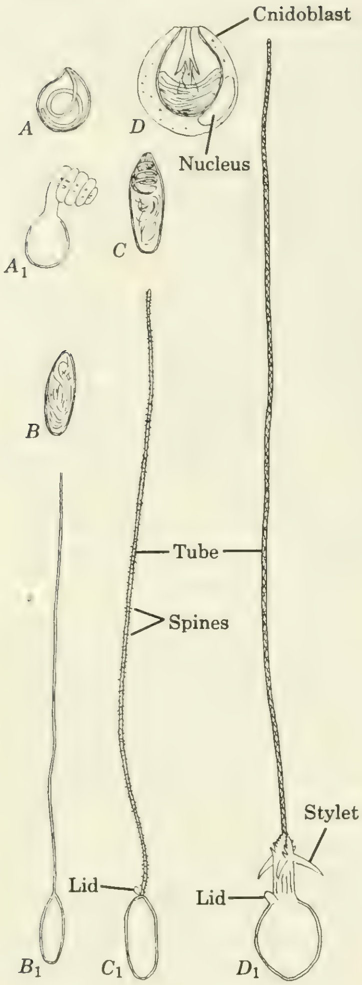


Fig. 10.4. The four types of nematocysts characteristic of all the hydras, shown undischarged and discharged. *A* and A_1, desmoneme; *B* and B_1, atrichous isorhiza; *C* and C_1, holotrichous isorhiza, with spiny tube; *D* and D_1, stenotele, the largest and most potent type. (Redrawn from L. H. Hyman, *The Invertebrates: Protozoa through Ctenophora*, copyright 1940 by McGraw-Hill Book Co., Inc., printed by permission.)

glass rod, or with a piece of blotting paper soaked in any of a variety of animal fluids, however, evokes immediate discharge. This evidence suggests that the diffusion of substances emanating from the prey in some way sensitizes the cnidoblast so that subsequent mechanical contact with the prey induces eversion of the thread. In contrast to the reactions of the cnidoblasts as independent effectors, the muscular responses of the tentacles in the capture of food appear to be coordinated by nerve cells, numerous in the epidermis and present in smaller numbers in the gastrodermis.

Among coelenterates in general, 17 different types of nematocysts have been recognized, and it has been found that the characteristics of these structures are useful in the classification of coelenterates. Some groups have only one type, and some types are found in only one or a few related groups. The hydras all have four types (Fig. 10.4): a large globular kind with conspicuous spines on the enlarged basal portion of the long thread, a small globular type with its thread always spirally coiled after discharge, and two small elongate types with long, straight threads. Examination of the bodies of animals paralyzed by hydras indicates that these nematocysts have different functions. The threads of the first type penetrate the body of the prey, even piercing the exoskeleton of small crustaceans; it is now apparent that this puncturing of the prey is very significant in the further feeding activities of the hydra (p. 295). Threads of the spiral type wrap themselves about fine projections, such as the bristles of a water flea. In some manner the nematocyst exerts a paralyzing influence on the prey. This action has been attributed to a poison, which is variously considered as being ejected from the free end of the hollow thread or as simply coating the outside of the everted thread. The exact nature of this poison has not been ascertained, although the name "hypnotoxin" has been applied to it. It is apparently composed of several different substances, and is probably not the same throughout the phylum.

The **gastrodermis** is the inner layer of cells lining the coelenteron. It consists chiefly of large cells which may bear one or two flagella (Fig. 10.3). These cells are capable of extending pseudopodia at their free ends to ingest particles of food from the coelenteron. As in the epidermis, these cells are epitheliomuscular in character; it was pointed out earlier that the arrangement of their muscle processes gives them an action antagonistic to that of the epidermal cells in contraction. In *Chlorohydra* the gastrodermal cells are crowded with green bodies regarded as unicellular plants. These cells live within the gastrodermis of the hydra and presumably pass from one generation to the next by transfer in the hydra's eggs. Similar plant cells, unicellular brown algae, or dinoflagellate protozoans inhabit the cells of many marine coelenterates, particularly some of the corals. The presence of such cells seems advantageous to the hydra, for in their autotrophic nutrition these simple plant or plant-like cells consume carbon dioxide and inorganic wastes and produce oxygen and organic compounds which are useful to the coelenterate host. Similarly, an advantage would seemingly accrue to the plant cells from the abundant raw materials produced as metabolic wastes by the cells of the host, as well as from the protected environment afforded the plants. A relationship of this sort, in which both organisms involved may be thought to benefit from the association, is termed **mutualism**. This is a particular manifestation of the broader phenomenon of **symbiosis**, interpreted as any situation in which the existence of one organism is closely involved in the existence of another. Mutualism may be contrasted with another kind of symbiosis termed **parasitism**, in which the advantage of the association is all on one side, and with **commensalism**, in which animals are associated merely as "messmates" without obvious advantage or disadvantage to either. The ciliated protozoans *Trichodina* and *Kerona*, often seen living on the outer surfaces of hydras, are probably commensals and not parasites.

In addition to the large gastrodermal epitheliomuscular cells, there are club-shaped **gland cells**, with the smaller end attached to the basement membrane and the larger end exposed to the digestive cavity (Fig. 10.3). These are located principally in the distal third of the body (the basal end is considered proximal) and presumably are the source of enzymes effective in extracellular digestion occurring in the coelenteron. A circlet of gland cells just within the mouth secretes something that seems to activate the other gland cells, indicating that even in this simple animal a rather complicated secretory cycle may exist. Scattered **sensory cells, nerve cells,** and some **interstitial cells** also occur in the gastrodermis.

The cells described in the epidermis and gastrodermis collectively constitute the **somatic cells** of the hydra. Cell specialization in this animal gives rise to different kinds of somatic cells, but it must be noted that the aggregation of these types into well-defined **tissues** has not progressed to any great extent. For example, the epitheliomuscular cells of the epidermis and gastrodermis combine the functions of epithelia and of contractile tissues, which in more advanced animals become the properties of separate and distinctly modified aggregations of cells. **Organs** are similarly primitive: only the tentacles may be termed organs in the accepted sense. Thus it may be stated that in the hydra there are different kinds of specialized cells, but that the differentiation of tissues and of organs is at a very low level.

The interstitial cells of the hydra constitute a sizable complement of apparently **totipotent** cells, capable of specialization in a variety of ways throughout the life of the individual. For example, interstitial cells are the source of cnidoblasts required for the replacement of discharged nematocysts. They are also important in the differentiation of a new hydra arising by budding, and in the regeneration of lost parts, for which these animals have a considerable capacity. Interstitial cells are, in addition, the source of the **germ cells** which appear at certain seasons. For all its simple organization, the hydra, with its several kinds of somatic cells, shows a great advance in cell specialization over such forms as *Volvox*, in which all the somatic cells are alike.

Metabolism. The small animals serving as food for the hydra, after being paralyzed and held fast by the nematocysts, are brought to the mouth by the tentacles and are **ingested** by engulfing movements of the hypostome. The mouth is capable of a surprising degree of distension to accommodate large objects of food. Soon after its ingestion the food is shifted by peristaltic contractions of the body to a position in the distal half of the coelenteron, where the early stages of digestion occur. Although no structural differentiation exists other than the abundance of gland cells in the distal region, there is apparently a physiological division of the coelenteron into gastric and intestinal regions; the food mass is never found in the more proximal or basal part of the cavity.

The process of digestion in the hydra is twofold. Enzymes released from the gland cells bring about the disintegration of the softer parts of the food mass, liquefying it and hastening its breakdown into particles. The soluble products of this **extracellular** phase of digestion are absorbed directly by the gastrodermal cells. Finely divided particulate matter is ingested by pseudopodia formed by the large gastrodermal cells and comes to lie in food vacuoles within their cytoplasm. Here the **intracellular** phase of digestion occurs, which is presumably entirely comparable with the process as it occurs in an amoeba. The indigestible residues are cast off by the gastrodermal cells and, together with the resistant parts of the food mass in the coelenteron, are expelled through the mouth by a series of violent contractions of the body. The bottom of a culture dish near a vigorous and well-fed hydra may often be littered with the egested exoskeletons of the water fleas upon which the animal has been feeding.

Although there is no circulatory system for the transfer and distribution of nutrients, it will be noted that no part of the body of the hydra is far removed from the source of food in the coelenteron. The wave-like contractions of the body tube, together with the activities of the gastrodermal flagella, maintain a circulation of the products of digestion within the coelenteron, which in recognition of its dual function is often termed the **gastrovascular cavity.** In colonial hydrozoans this distributive function of the common coelenteron pervading the entire branching colony is very important in the nutrition of all the component individuals. Soluble products of digestion undoubtedly reach epidermal regions by diffusion across the short intervening distances.

Oxygen reaches all the cells by diffusion from the external medium. As in all animals it is used in cellular metabolism, which releases energy and produces as by-products carbon dioxide, water, and nitrogenous wastes. In animals as small as the hydra, **excretion** probably occurs over the general body surface; there are no specialized organs of excretion.

Responsiveness. All movements of the hydra are the result of contractions by the longitudinal and circular muscle processes of epidermal and gastrodermal cells. The varied positions and shapes which the animal may assume indicate that these processes can contract and relax locally as well as over the entire body, and that they react in a coordinated fashion. In addition to extensions and contractions of body and tentacles as a whole, there are peristaltic movements; these may be very slow, or they may be rapid, as when egesta are violently expelled, or when food is quickly moved from one region of the coelenteron to another. The circular muscle processes function as sphincters about the mouth and at the base of each tentacle.

Locomotion occurs in a variety of ways. A hydra may move by imperceptible degrees, gliding upon its base. It may extend itself horizontally until the tentacles are in contact with the surface, release the base, which is then drawn to a new point of attachment, and extend the tentacles once more, repeating the process. Again, the hydra may attach the tentacles, release the base, and move by a series of slow somersaults (Fig. 10.5). It can also walk clumsily upon its tentacles with the body free and contracted. The habit of some hydras of floating at the surface with the base clinging to the surface film has already been mentioned.

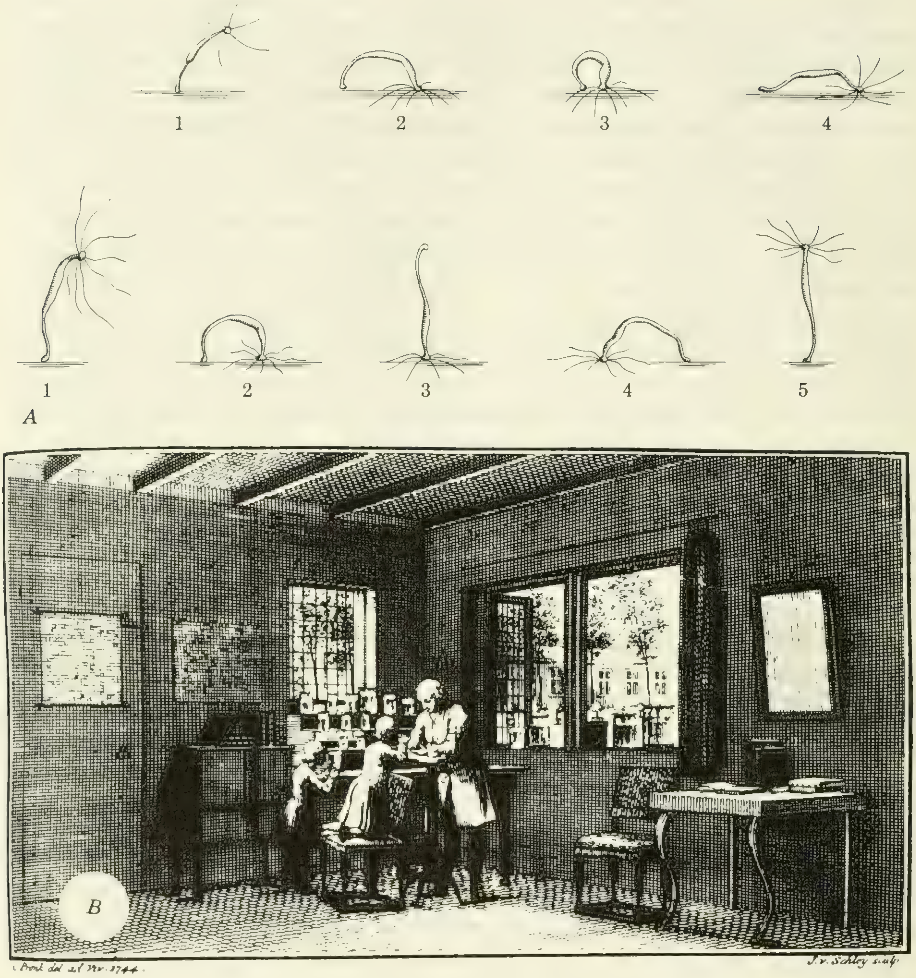


Fig. 10.5. *A*, locomotion in *Hydra*. *Above*, "inchworm" locomotion, in which the distal end is applied to the substratum and the basal end drawn up to attach beside it. *Below*, "somersaulting" locomotion. Numbers indicate successive positions. *B*, Abraham Trembley, the first serious student of hydras, with his young pupils. (*A*, redrawn, and *B*, reproduced directly, from Abraham Trembley, *Histoire de Polypes*, Leyden, 1744. This monograph contains the earliest published accounts of the details of locomotion, feeding, and reproduction in hydras, masterful experimental studies of regeneration, and the first demonstration of the animal nature of the polyps. See also Figure 12.13, p. 362.)

The characteristic movements and reactions involved in feeding are well coordinated. When a water flea or other small organism has been captured by a single tentacle, the other tentacles usually take part in the transfer of the prey to the mouth; however, a very small animal may be caught and transferred to the mouth by one tentacle alone, without reactions by the others. The mechanisms underlying feeding reactions have only recently been elucidated. It has been demonstrated that the hydra opens its mouth to engulf prey only after the attacked organism has been punctured by the discharge of the large, barbed nematocysts. This suggests that the puncture of the prey releases some substance into the water, and that the hydra reacts to the presence of this substance by opening its mouth and executing engulfing movements of the hypostome. Following this line of reasoning, investigators have found only one specific chemical compound, reduced glutathione, which is normally present in the body fluids of animals upon which hydra feeds and will elicit the feeding reaction in hydras. Animals such as other hydras, which the hydra never attacks or attempts to ingest, do not contain this substance; but if a hydra is exposed to a minute amount of reduced glutathione in the culture medium it will engulf other hydras, or in the absence of food will open its mouth so widely that it turns inside-out. The operation of the mouth and hypostome in engulfing food brought in by the tentacles is certainly a coordinated response, and the reactions are probably set off by certain neurosensory cells which are stimulated by very low concentrations of reduced glutathione emanating from injured prey. The general behavior of the individual is influenced by its physiological state; hydras kept for a short time without food are much more responsive in their feeding reactions than well-fed animals.

In addition to its specific reaction to reduced glutathione, the hydra reacts to mechanical contacts—light, heat, and electrical stimulation. The effective stimuli in the normal behavior of the animal are probably combinations of specific environmental changes, conditioned by the physiological state of the individual at any given time. Responses to combinations of stimuli can be more easily studied in some of the larger coelenterates. The hydrozoan jellyfish *Gonionemus*, for example, reacts moderately to contact with objects, to objects in motion, and to chemical compounds such as acids in solution, but the reaction is greater when these stimuli are presented in combination. Thus, the tentacles of a resting *Gonionemus* are somewhat sensitive to the contact of a fine pipette which merely touches them or is moved along their surface, and to meat juice gently ejected against them without movement of the pipette. But when the pipette is drawn rapidly along a tentacle as the juice is ejected, the entire animal goes into action. All the tentacles twist and turn, bending toward the mouth; the hypostome turns toward the tentacle stimulated, and nematocysts are discharged. This combination of stimuli is presumably like that received from a small fish or crustacean, which would normally be attacked, for the reactions are similar in the two cases.

We may now turn to an examination of the cellular organization of the **sensory-neuro-muscular** mechanism, the physical basis for the reactions which have been described. The epidermis contains many **nerve cells,** or neurons, and at least four different kinds of **sensory receptor cells,** all connected with the contractile processes of the large epidermal epitheliomuscular cells. In addition there are **neurosensory cells,** so termed because they resemble nerve cells and have processes, presumably involved in sensory reception, extending to the outer surface of the epidermis. Nerve cells and receptors are also found in the gastrodermis, although in smaller numbers. The epidermal and gastrodermal elements are generally considered as forming two networks, apparently rather sparsely interconnected by neurons traversing the supporting lamella. The richer innervation of the epidermal longitudinal musculature is reflected in the greater degree of coordination of its activities, as compared with those of the gastrodermal circular musculature.

The nature of the coelenterate sensory-neuro-muscular system has been the subject of much disagreement among zoologists. The controversy has centered about the question whether the network of neurons represents a morphological continuum, composed of cells whose processes are actually physically continuous with each other, or whether the extremities of adjacent neurons are merely in synaptic contact as in the nervous systems of all higher animals. Reliable evidence bearing upon this question is difficult to obtain in an animal as small as the hydra, but it is probably safe, where necessary, to extend to the hydra the results of studies on larger coelenterates. Modern research has demonstrated almost beyond question that the network is not continuous, and that nerve impulses traveling through the system must pass from cell to cell across a discontinuity, or **synapse** (pp. 96–100). Although the processes of adjacent neurons may be in contact or actually intertwine with each other, there seems to be no protoplasmic continuity between them. If this is true, it probably follows that the passage of a nerve impulse across a synapse in coelenterates, as elsewhere in the Animal Kingdom, involves the secretion by the neuron of a chemical mediator which excites the adjacent neuron.

However this system may thus seem to agree, in its basic mechanism, with those of more advanced animals, there are two fundamental and interrelated differences which emphasize its primitive nature. One is the fact that this is a diffuse, net-like system, with no indication of the formation of **ganglia**, the aggregations of nerve cells so characteristic of the nervous systems of all higher forms. The other is the fact that the neurons and synapses of coelenterates conduct impulses in any direction with apparently equal facility; in other words, there is no indication here of polarization within the nervous system. In higher animals conduction within one neuron may occur in either direction, but the neuron is polarized in the sense that the impulse can be propagated across a synapse at only one end. This is the basis of the one-way transmission characteristic of the nervous systems of animals more advanced than coelenterates. In the hydra and its relatives a nerve impulse must be conducted over a long pathway, wandering along the branching processes of widely spread neurons, possibly exciting inappropriate connections along the way. In contrast to this, a ganglionated system, with polarized synapses, offers the special advantages of contiguity of nerve cell bodies interconnected by short processes, promoting the channelization of impulses with greater efficiency along definite pathways. Although the coelenterates do not approach this level of specialization, functional elements constituting a "nervous system" do occur and are somewhat more highly organized than those of sponges (p. 280).

If we recall the definition of responsiveness as the capacity, inherent in living cells, of responding to stimuli or changes in the environment, it is apparent that the foundation of behavior in the hydra, as in a vertebrate or in a protozoan, is the responsiveness of cells. All the cells of the hydra are capable of responsiveness, but those of the sensory-neuro-muscular system are specialized in this respect. Although experiments which have demonstrated the nervous functions of larger animals cannot be performed with an animal as small as the hydra, the functions of certain cells can be inferred from their relationships and from our knowledge of the reactions of similar cells in other animals. Reception of stimuli and establishment of nerve impulses by the sensory cells, conduction and discharge of impulses by the neurons, and the resultant action of effectors such as contractile and secretory cells all occur in the hydra.

If a "system" is defined as a "group of organs" performing some general function, the hydra has no nervous system. Yet, we naturally speak, as in the foregoing discussion, of the "nervous system" in hydra. In general, the nervous mechanism of coelenterates is a **receptor-effector** system, in contrast with the **receptor-adjustor-effector** systems of higher animals (Fig. 10.6). Further comparisons of the mechanisms of coordination in animals will be deferred until after the nervous system of the earthworm has been described in Chapter 14. The organization of this mechanism in annelids is intermediate between that of coelenterates and that of vertebrates.

Reproduction and Development. At certain seasons of the year, particularly in autumn, hydras reproduce by **syngamy**, the union of gametes. The **testes** are usually located on the distal half of the trunk, the **ovaries** near the middle. Testes may appear first and ovaries later on the same animal, or both may be present together. Animals in which the same individual possesses both ovaries and testes are said to be **hermaphroditic** or **monoecious**.

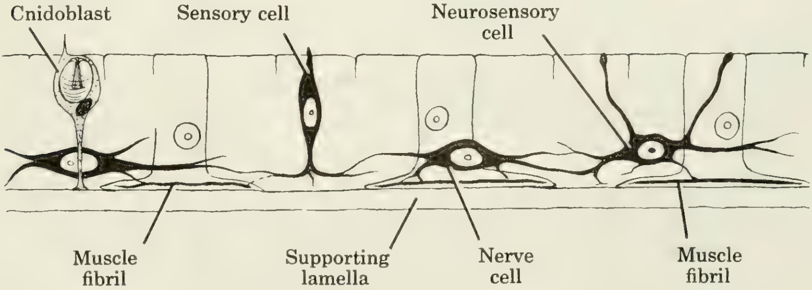


Fig. 10.6. Diagram of the relationships of the sensory-neuro-muscular system in the epidermis of *Hydra*. One of the nematocysts, considered independent effectors, is included. The muscle fibrils occupy the basal processes of large epitheliomuscular cells.

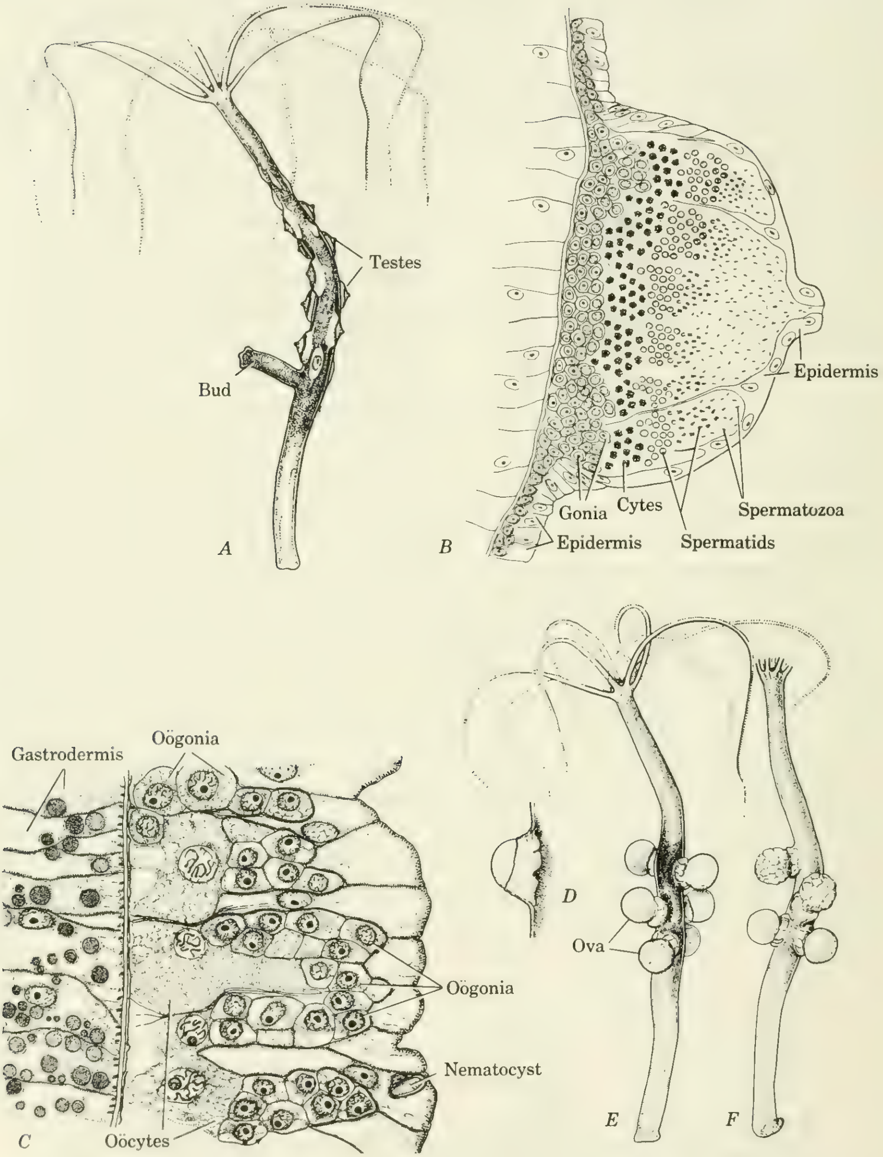

Testes
Bud
A
Epidermis
Gonia
Cytes
Spermatozoa
Epidermis
Spermatids
B
Gastrodermis
Oögonia
Oögonia
Nematocyst
C
Oöcytes
D
Ova
E
F

Fig. 10.7. Aspects of sexual reproduction in *Hydra attenuata*. *A*, male with well-developed testes (and a young, asexual bud). *B*, longitudinal section of a single testis showing stages in maturation of gametes. *C*, longitudinal section through a portion of an ovary, showing stages in oögenesis. *D*, a mature ovum resting in the remains of the ovary. *E*, female bearing six mature ova. *F*, female bearing fertilized eggs, two of which are undergoing cleavage. (From P. Brien and M. Reniers-Decoen, 1951, *Annales de la société royale zoologique de belgique*, vol. 82.)

Monoeciousness may be the usual condition in hydras, although species in which the individuals seem to be exclusively male or female, hence **dioecious**, have been reported. There are no secondary sexual characteristics in hydras; only by observing the testes or ovaries can the sex of an individual be determined. These **gonads** appear as swollen protuberances from the epidermis in the characteristic regions (Fig. 10.7). Within them, **ova** or **spermatozoa** arise from interstitial cells. Fully matured spermatozoa may be seen moving actively within the testis; they are discharged by the periodic opening of the apex of the testis, which thus liberates successive swarms. The spermatozoon then swims about until it dies, or until it comes into contact with an ovum which has been exposed by the rupture of its epidermal covering. The zygote formed by the union of these two gametes undergoes cleavage and secretes about itself a shell-like cyst, or **theca**. Within the theca, development proceeds until an outer layer of cells, the ectoderm, and an inner solid mass, the endoderm, have been formed. The embryo within its theca then becomes detached from the parent and drops to the bottom. Tentacles eventually develop; the embryo breaks from its cyst, becomes attached, develops a coelenteron, forms a mouth, and so becomes a miniature hydra. Zygotes developing in late autumn pass the winter within the protective cyst.

Hydras frequently produce new individuals by **budding**, a process referred to as asexual reproduction (Fig. 10.8). It is, essentially, reproduction by cell division. It differs, however, from the asexual reproduction of protozoans in that the mass of new cells produced is organized by some integrating influence into a multicellular individual with the characteristics of the parent. There is first an accumulation of nutrient material in the gastrodermal cells at some place toward the middle of the body, and cells in the epidermis of this region divide repeatedly to form a bud-like swelling. An extension of the coelenteron grows into the bud, which then appears as a blindly ending outgrowth of the two layers of the body wall. Tentacles appear as evaginations of epidermis and gastrodermis, and finally a mouth is formed. If food is abundant, the bud may remain attached to the parent for some time, and in exceptional cases it may rebud to form several generations in a branching system. Usually, however, the connection between parent and offspring becomes constricted, and the bud is detached as an independent individual as soon as the tentacles and mouth become functional.

Growth and Regeneration. Recent research has demonstrated the interesting fact that a region just below the hypostome of the hydra constitutes a zone of proliferation. In this area new cells are constantly being produced by mitotic activity and added to the layers making up the body wall. There is a constant slow progression of cells downward toward the base; the oldest cells in the body make up the base itself and are gradually sloughed off at this point. Thus, the base and the portions of the stalk adjacent to it are composed of aged, "exhausted" cells, whereas a continuous cycle of replacement provides young, vigorous cells in the more distal regions.

Like many other types of animals with simple organization and well-

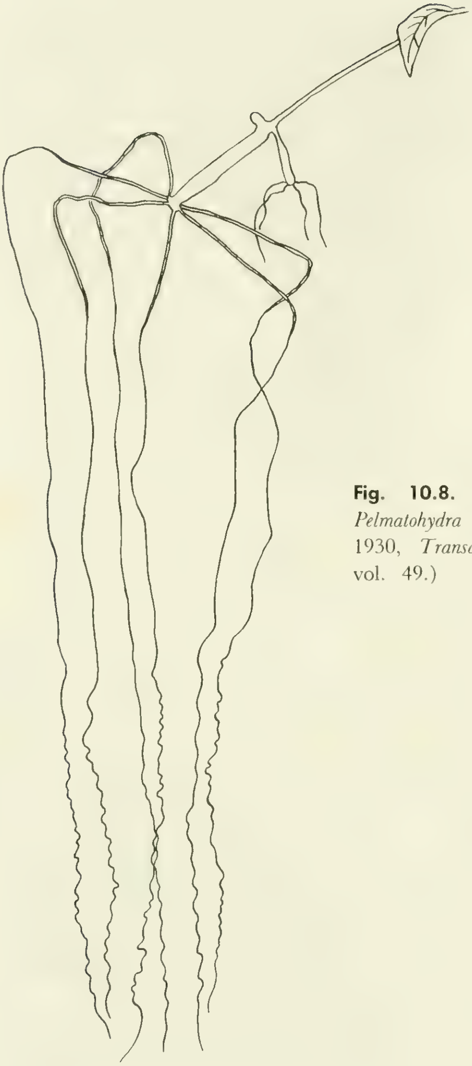


Fig. 10.8. Asexual reproduction by budding in *Pelmatohydra oligactis*. (Redrawn from L. H. Hyman, 1930, *Transactions of the American Microscopical Society*, vol. 49.)

developed powers of asexual reproduction, hydras and the coelenterates in general have a marked capacity for regeneration. When a hydra is cut transversely into two pieces, a new basal part appears on the piece having tentacles, and new tentacles, mouth, hypostome, and zone of proliferation develop at the distal end of the basal piece. In a few days two complete hydras will have been formed and will have gradually assumed the normal proportions. As might be expected from knowledge of its peculiar cellular constitution, the extreme basal region has very limited powers of regeneration. In more distal regions, however, regeneration and subsequent growth of new individuals occur even when the animal is cut into several small pieces.

The Hydroids and Hydromedusae. With few exceptions, among which the hydras are notable, the Hydrozoa are marine animals. They are attached in at least one phase of the life cycle, and most species form colonies of individuals variously specialized in correlation with feeding, protection, and reproduction. The life cycle in some species, but not in the majority, includes a free-swimming jellyfish stage or hydromedusa. The species *Obelia geniculata* (Fig. 10.9) is representative of those that do present this feature. In its hydroid ("hydra-like") phase or generation this species is a colony containing possibly thousands of individuals, or **polyps**, each individual comparable with a single hydra and all united as the buds of a hydra would be if they did not become detached. The obelia colony in fact begins as a single polyp, which grows and buds repeatedly until it consists of many upright stems bearing polyps and arising from the root-like **hydrorhiza** ("hydra root") growing

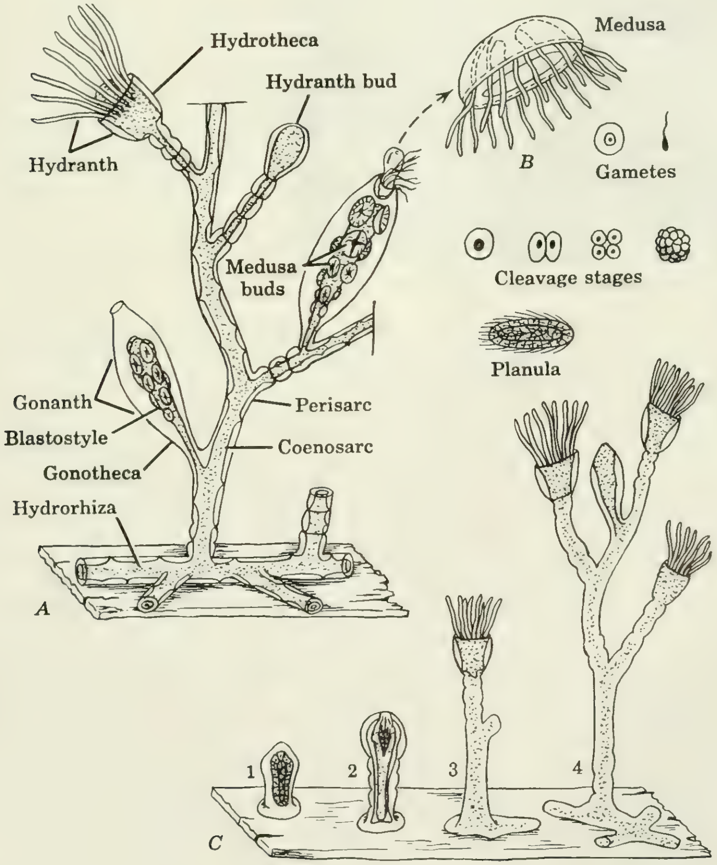

Hydrotheca
Hydranth bud
Medusa
Hydranth
B
Gametes
Medusa buds
Cleavage stages
Planula
Gonanth
Perisarc
Blastostyle
Coenosarc
Gonotheca
Hydrorhiza
A
1
2
3
4
C

Fig. 10.9. *Obelia:* structure and life cycle. *A*, portion of a colony of the hydroid generation. *B*, medusa, and sexual reproduction. *C*, growth of a young hydroid colony from the attachment of a planula larva; numbers indicate successive stages of growth.

along the surface of attachment. In the fully developed colony there are two types of individuals: (1) **hydranths,** which have mouths and tentacles, and coelenterons continuous with the tubular cavity pervading all the stems of the colony; and (2) **gonanths,** modified polyps without either mouths or tentacles, consisting chiefly of a central, rod-like **blastostyle** upon which are formed the buds which become free-swimming **medusae.** Both hydranths and gonanths are surrounded by appropriately shaped secreted containers, known respectively as **hydrothecae** and **gonothecae,** which are specialized portions of the **perisarc** surrounding the entire colony. The living material, continuous throughout the colony, constitutes the **coenosarc.**

The obelia colony, with its clearly marked **dimorphism** ("two forms"), thus arises by a process of repeated budding involving also the differentiation of the two types of polyps. The medusae, or jellyfishes, which constitute the products of asexual reproduction in the gonanths, are specialized in yet another direction—for swimming and sexual reproduction. After their release from the parent gonanth they reach sexual maturity as males or females, having either testes or ovaries. The gametes produced in these gonads are released into the water, where fertilization occurs. The resulting zygote develops into a ciliated, solid-bodied, two-layered, free-swimming stage, the **planula,** which settles to the bottom and transforms into an attached polyp from which a new colony is formed. In *Obelia*, sexual reproduction is carried on only by the medusa generation, and asexual reproduction is limited to the hydroid generation. Thus, we may say that there are two generations which alternate; the term **metagenesis** is sometimes applied to such alternation of generations. The medusae formed by hydroid colonies, and other similar medusae, are called hydromedusae to distinguish them from the larger, more specialized jellyfishes belonging to the class Scyphomedusae.

Not all the genera of the Hydrozoa exhibit alternation of generations. Some colonial forms develop reduced or degenerate medusae, often called **gonophores,** which are never released but which develop gonads and produce gametes while still attached. In other genera such fixed medusae grade into special gamete-forming structures termed **sporosacs;** in still others, as in the solitary hydras, the gonads develop directly on the polyps, without a trace of the medusoid generation. In the opposite direction lie such forms as (1) *Gonionemus*, with a large, free-swimming medusa produced by a minute polyp which scarcely buds except to generate the medusa; and (2) *Liriope*, in which the planula develops directly into the medusa without a trace of the polyp. The entire assemblage of hydrozoans may be arranged in a regular series, with exclusively polypoid forms like *Hydra* at one extreme, and exclusively medusoid forms like *Liriope* at the other. In such a series *Obelia*, with its polypoid and medusoid generations about equally represented, lies in the center. It may be suggested that this kind of a series probably represents an evolutionary sequence, but the direction of evolutionary change is a matter of conjecture. It seems illogical, however, to consider *Hydra* a primitive stem form; it is one of the very few fresh-water hydrozoans, is non-

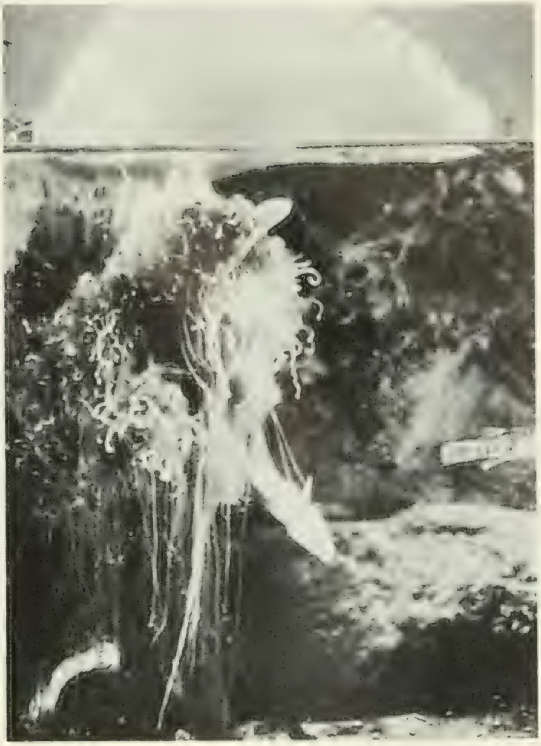


Fig. 10.10. A siphonophoran, *Physalia*. The entire colony is suspended below the float. Several small fishes have been snared and killed by dactylozooids and are being drawn up for ingestion and digestion in gastrozooids. (Photograph by George Lower.)

colonial, and shows a remarkably telescoped pattern of development, without medusae or planulae. It is preferable to assume that planula-like ancestors developed into medusae, and that the polypoid stages represent original larval forms which have persisted and become, in many cases, reproductive stages.

Other Hydrozoa. Related to the hydroids and hydromedusae are the hydroid corals, or **Hydrocorallinae.** These have a massive skeleton of carbonate of lime, somewhat resembling the skeleton of true corals. Other interesting types are the **Siphonophora,** shown by the fossil record to be an extremely ancient group, of which the "Portuguese man-of-war," *Physalia*, is the most familiar example (Fig. 10.10). *Physalia* is a colony of specialized individuals, sometimes spoken of as "persons," having a gas-filled float supporting the whole. The colony closely resembles an individual organism, with organs specialized for various functions such as food-getting, digestion, reproduction, and so on. Actually, the "organs" are individual members of the colony, each specialized to perform a particular function. Such a group may be spoken of as **polymorphic,** in contrast to **dimorphic** colonies like those of *Obelia*. The individuals that function as tentacles (**dactylozooids**) are laden with nematocysts which can affect the human skin very severely. These "persons" capture such prey as small fishes and crustaceans, which are then drawn up to the digestive polyps, or **gastrozooids,** near the float. There are

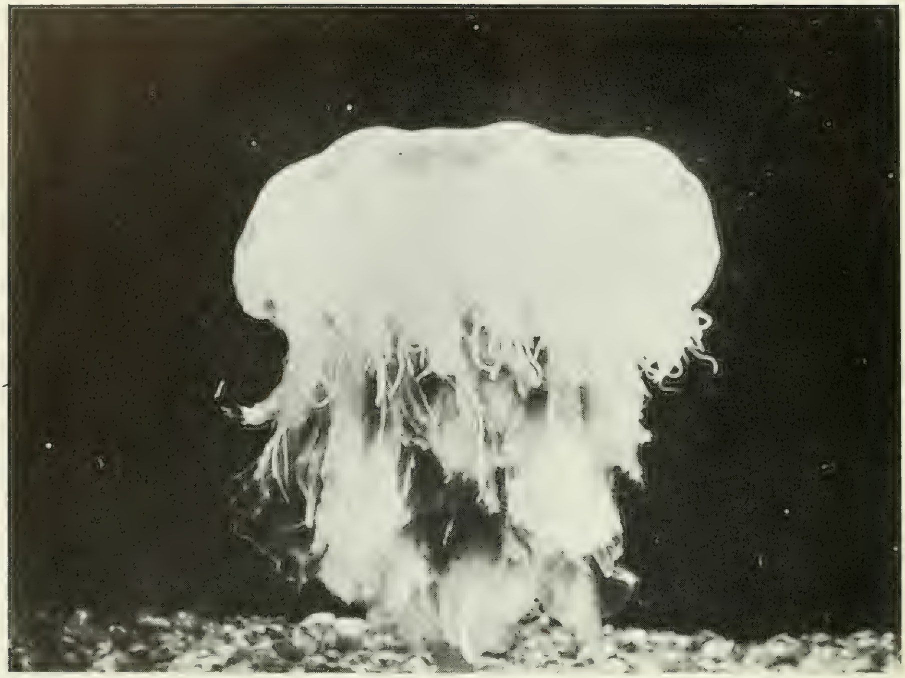


Fig. 10.11. A scyphomedusan jellyfish, *Cyanea*. (Photograph by George Lower.)

also **gonozooids**, medusa-like individuals which are not released but produce gametes. The siphonophores are considered to have diverged from the main hydrozoan stem early in its evolution.

THE CLASS SCYPHOMEDUSAE

Most of the jellyfishes called hydromedusae are small, like *Gonionemus*, or smaller. The jellyfishes comprising the class **Scyphomedusae** are mostly of a larger size; individuals of the species *Cyanea arctica* (Fig. 10.11) have been recorded with a diameter of 12 feet and tentacles over 100 feet in length. The amount of solid or living material in such individuals would be small, however, because jellyfishes are composed chiefly of water. The bulk of their substance consists of the "jelly," which in these forms is a gelatinous mass conspicuously provided with cells resembling connective-tissue elements of higher animals. The jelly itself may thus be considered as intercellular material, comparable with the fibrous substance of connective tissue or the ground substance of cartilage. In scyphomedusans specialized organs of equilibration, termed **statocysts**, are located at intervals around the margin of the bell; these sense organs are important in the free-swimming locomotion of jellyfishes, and similar though simpler statocysts occur also in hydromedusae.

The genera *Cyanea* and *Aurellia* are representative Scyphomedusae found in North Atlantic waters. In typical cases the life cycle of a scyphomedusa consists of the following sequence (Fig. 10.12): a planula larva develops from a zygote; this larva produces an attached polyp generation, the **scyphistoma,** from which free-swimming medusae arise in succession by transverse budding or **strobilization.** The young medusae released from the strobila are saucer-like individuals called **ephyrae;** they grow and transform into adult, sexually reproducing jellyfishes. Asexual reproduction of the polypoid generation, by budding to produce additional polyps, has also been reported.

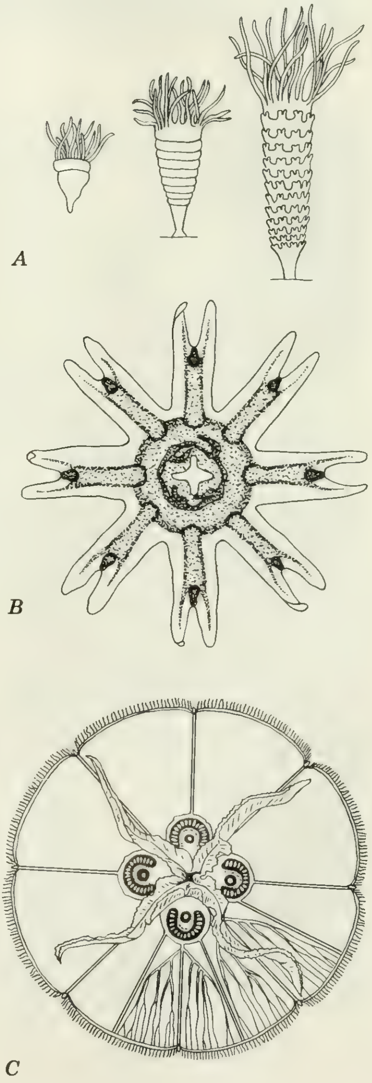


Fig. 10.12. Structure and life cycle of Scyphomedusae. *A*, polyp stage, or scyphistoma, of *Cyanea*, developed from a planula larva, and two **strobilas** undergoing asexual reproduction, giving rise to many ephyrae. *B*, ephyra, or immature medusa, probably of *Chrysaora*. *C*, mature jellyfish or medusa stage of *Aurellia*. The bell of this medusa is traversed by many gastrodermal canals, shown in only one quadrant; the margin bears many short tentacles as well as marginal sense organs. The gonads are prominent semicircular structures borne beneath the radial canals; the oral tentacles are long and flexible and are the structures chiefly used in feeding. (*A*, redrawn from J. J. Steenstrup, *Ueber den Generationswechsel*, Copenhagen, 1842. Steenstrup was among the first to understand the significance of alternation of generations in such animal groups as coelenterates and parasitic flatworms. *B* and *C*, redrawn from L. H. Hyman, *The Invertebrates: Protozoa through Ctenophora*, copyright 1940 by McGraw-Hill Book Co., Inc., printed by permission.)

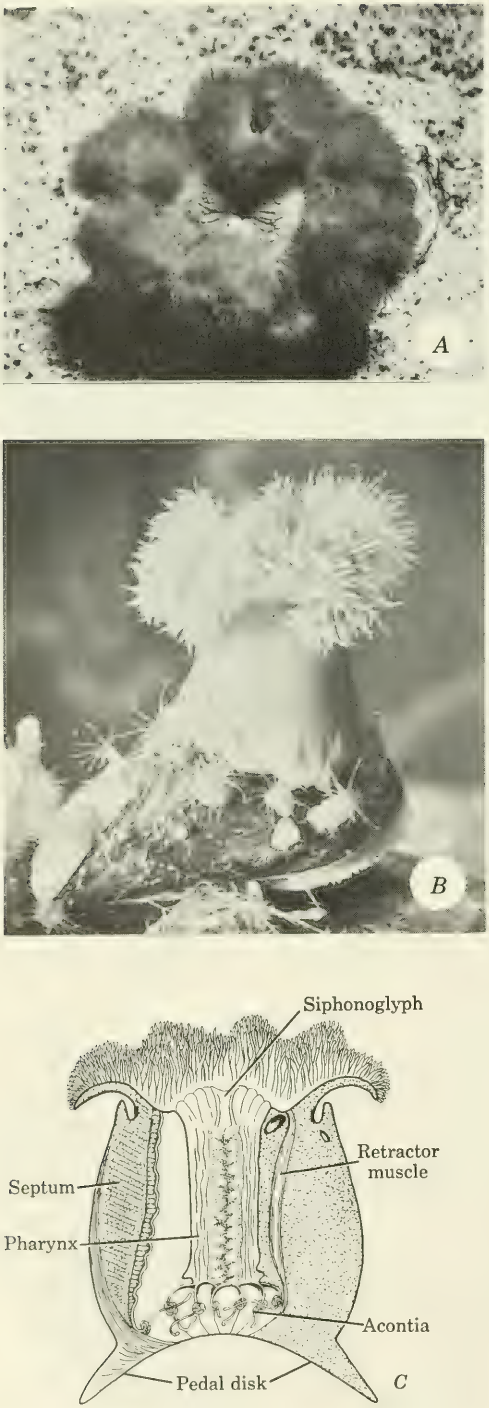


Fig. 10.13. *Metridium dianthus*, a sea anemone. *A*, oral view of a large specimen, showing oral disk, mouth, tentacles, and siphonoglyph. *B*, a mature individual attached to the shell of a mussel; the young individuals about its base were produced asexually by "pedal laceration," developing from small pieces detached from the base of the parent. *C*, diagrammatic longitudinal section; the so-called **complete** septa extend from the body wall to the pharynx, and **incomplete** septa have free edges in the coelenteron, containing numerous gland cells and nematocysts. The **acontia** are filamentous continuations of these septal edges. (*A* and *B*, photographs by Bassett Maguire, Jr.; *C*, redrawn from L. H. Hyman, *The Invertebrates: Protozoa through Ctenophora*, copyright 1940 by McGraw-Hill Book Co., Inc., printed by permission.)

THE CLASS ANTHOZOA

The Anthozoa are represented by the sea anemone, *Metridium dianthus*, whose solitary individual polyps are common along the New England coast. As in anthozoans generally, the sea anemone is provided with a somewhat flattened oral disk surrounded by tentacles (Fig. 10.13). The epidermis turns in at the mouth and hangs downward into the coelenteron to form a tubular **pharynx** or **stomodaeum.** This pharynx is attached to the lateral body wall by a series of radiating partitions or **septa**, which thus divide the upper part of the coelenteron into radial compartments, continuous with the undivided cavity below. The biradial symmetry characteristic of many Anthozoa is produced by the presence of one or more heavily ciliated grooves or gutters, called **siphonoglyphs**, traversing the pharynx longitudinally from its outer to its inner edge. These grooves presumably function to provide active currents of fresh, aerated water to the inner parts of the animal, and to flush away wastes.

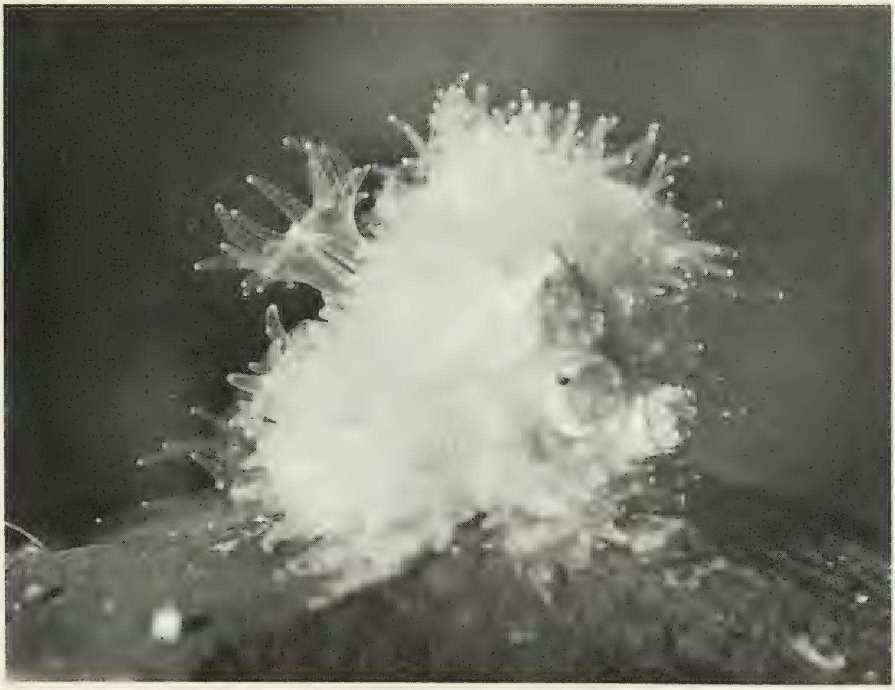


Fig. 10.14. A stony coral, *Astrangia danae*. Each individual occupies a cup-like portion of the calcareous base. In the expanded individual, note the groups of nematocysts on the tentacles, and the edges of the septa in the coelenteron. (Photograph by Bassett Maguire, Jr.)

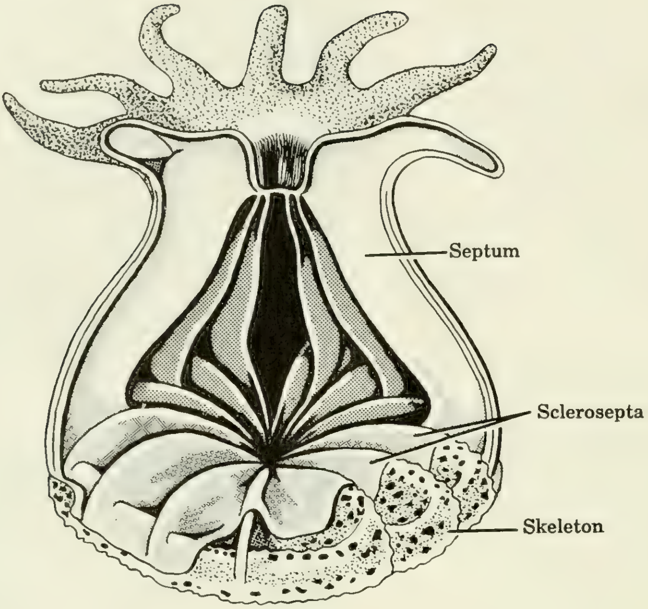


Fig. 10.15. An individual stony coral, showing the relationship between the animal and its calcareous skeleton. (Adapted from K. von Frisch, 1953, *Biologie*, vol. 2, by permission of Bayerischer Schulbuch-Verlag.)

Other representative anthozoans are the true corals, such as *Astrangia danae*, a northern coral (Fig. 10.14), and the many species abounding in tropical seas. The coral individual resembles a small sea anemone lying in a limy, cup-like skeleton secreted by its epidermal cells. The stony mass of a coral head or reef, covered completely by the living substance of its polyps, is contributed to by the secretory activites of large numbers of these individuals, producing skeletal material beneath them and forming new polyps by budding or subdivision as the size of the mass increases. The living individuals are found only at the surface (Fig. 10.15); the underlying stony material is uninhabited, except as it may be invaded by a variety of worms, crustaceans, bivalves, and other animals of the reef. The part played by corals (Fig. 10.16) in the formation of coral islands and of the limestone in various deposits has given these coelenterates an important role in geologic history.

Other anthozoan types are numerous, such as the sea pens, sea fans, and many others (Fig. 10.16). All are marine, and many produce skeletons to a considerable degree, of either organic or inorganic materials. Anthozoans have in common the fact that no free-swimming medusoid stage is found in their life cycles. In sexual reproduction gametes are produced by the sessile polyps, and a new generation develops from the resultant planulae.

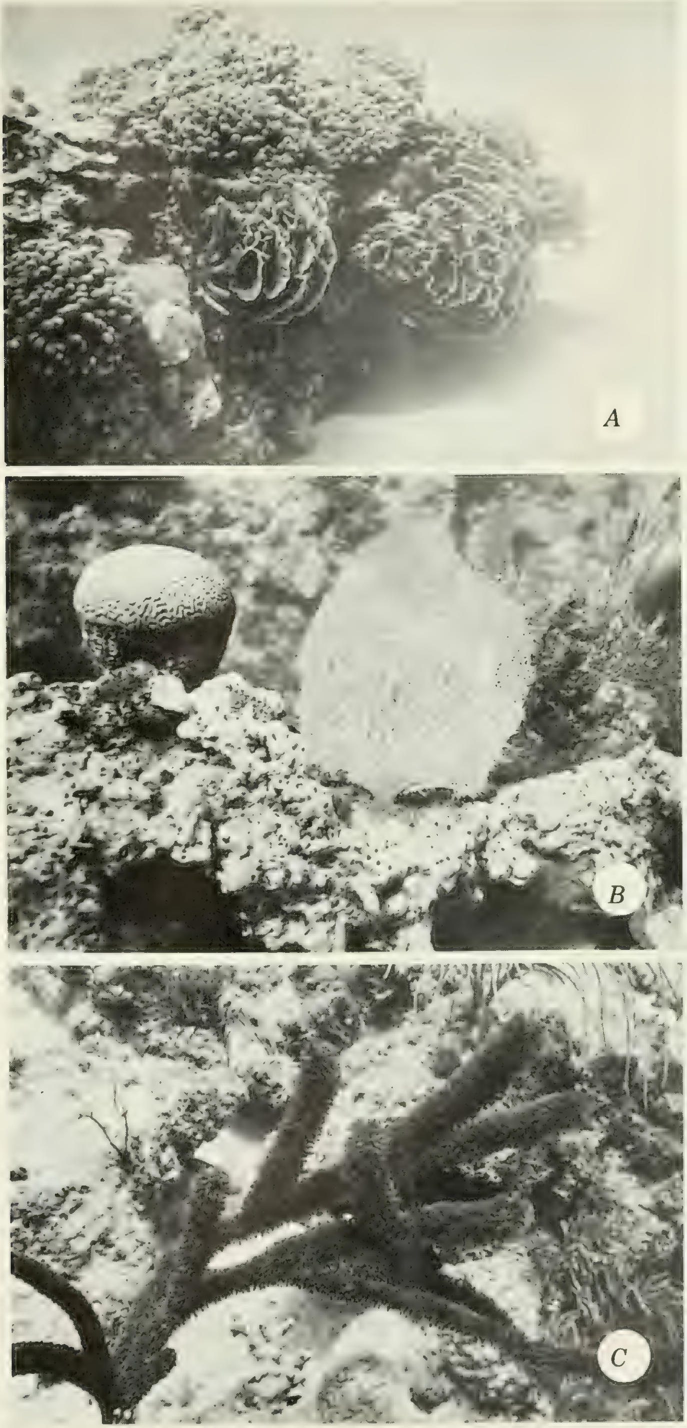


Fig. 10.16. Anthozoa: *A*, portion of a Bahamian coral reef, showing two species of coral with contrasting patterns of growth. The knobbed coral is *Porites porites;* the lettuce coral is *Agaricia agaricites*. *B*, a brain coral, *Meandrina*, and a sea fan, *Gorgonia*. *C*, portion of a gorgonian colony, showing individual polyps expanded. (Underwater photographs by John F. Storr.)

The Coelenterate Body Plan

In the simplest coelenterates the body is like a sac with a wall composed of two layers, the epidermis and the gastrodermis; hence the animals are called diploblastic. The single opening into the coelenteron, termed the mouth although it functions as both mouth and anus, is surrounded by tentacles. The radial symmetry characteristic of the phylum is obvious in most species. In the more specialized coelenterates there is a middle region, between epidermis and gastrodermis, which may have several kinds of cells and may then be termed a mesenchymal layer, of mesodermal origin. Such coelenterates are more properly called triploblastic than diploblastic animals. Compared with sponges, the coelenterates are evidently animals of more complex type; compared with vertebrates, however, they are very primitive. They have, nevertheless, important features in common with all the higher phyla. If comparisons are made between cell layers, it will be seen that the epidermis of the coelenterate is comparable with the outer layer of the skin of a vertebrate and the gastrodermis with the lining of the digestive tract. The parts of the body derived from mesoderm in such forms as vertebrates are absent, except insofar as the middle region in many coelenterates may be cellular and thus comparable with the mesenchyme of higher forms.

Their relatively simple, primitively two-layered construction, with what may be called tissues but without well-developed organs, together with their basic radial symmetry and their coelenteron with only one opening, constitute consistent features which make it possible to set the coelenterates apart from the more advanced Metazoa.

The Phylum Ctenophora

The Ctenophora, commonly known as sea walnuts or comb jellies, are animals with biradial symmetry, epidermal and gastrodermal layers like those of coelenterates, definite muscular elements and a mesenchymal middle layer (collenchyme) that are both derived from mesoderm, and eight meridional rows of swimming plates or combs formed of fused cilia. Ctenophores are all small marine animals which float and swim near the surface, although a few aberrant species that have become adapted to a creeping existence upon the bottom are known. The free-swimming forms are sometimes present in such tremendous numbers that they constitute an important element in the floating life of the ocean. Their food consists of whatever small animals they may capture with the aid of the tentacles which some ctenophores possess, or with the parts related to the mouth. Abundant mucous secretions of the epidermis aid in trapping small animals which are then driven toward the mouth by ciliary currents. In contrast to the coelenterates, ctenophores lack nematocysts, but some possess **adhesive cells** on the tentacles which hold fast to

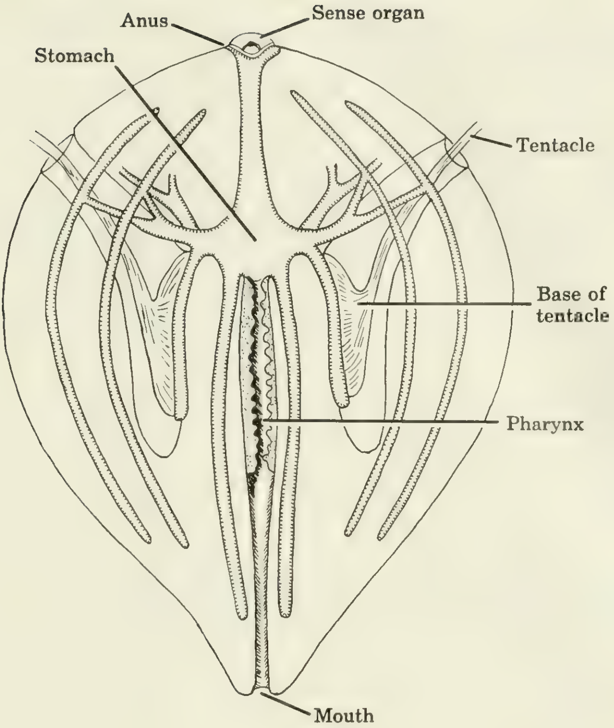


Fig. 10.17. General structure of a ctenophore; diagrammatic. The characteristic rows of ciliary combs, as well as the external portions of the tentacles, have been omitted. (Redrawn from L. H. Hyman, *The Invertebrates: Protozoa through Ctenophora*, copyright 1940 by McGraw-Hill Book Co., Inc., printed by permission.)

the prey until it can be drawn into the mouth. The gastrovascular cavity is divided into **pharynx, stomach,** and branching **diverticula** which ramify extensively throughout the body. A small anus is present at the aboral end. The resemblances between coelenterates and ctenophores are thus rather superficial and are considered insufficient to warrant placing these groups in the same phylum.

As shown by Figure 10.17, the structure of a ctenophore is rather complicated for an animal whose basic organization is so simple. The eight rows of combs, responsible for the name Ctenophora ("comb bearers"), are a unique feature of the phylum. Each row consists of a series of comb-like plates composed of fused cilia; the combs are found in all members of the phylum except a few, where they are lost or modified in the course of development. Locomotion is effected by the beating of the combs, which has been much studied as an example of ciliary action controlled by a nervous system. In addition to a coelenterate-type nerve plexus throughout the body, nervous elements are concentrated beneath the ciliary rows.

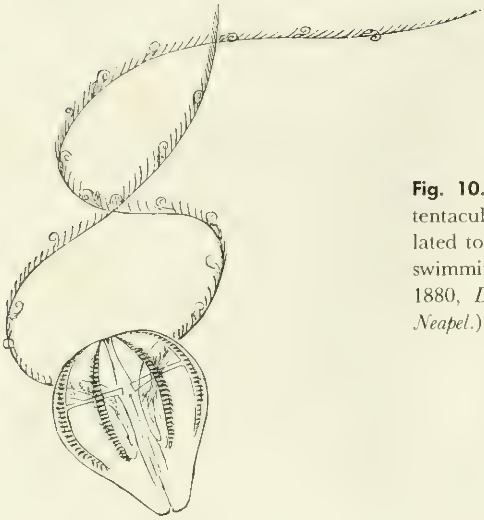


Fig. 10.18. *Hormiphora plumosa*, a tentaculate ctenophore closely related to *Pleurobrachia*, in its normal swimming attitude. (After C. Chun, 1880, *Die Ctenophoren des Golfes von Neapel.*)

Representative Types. Common and representative genera to be found along our North Atlantic seaboard are *Pleurobrachia*, with tentacles (Fig. 10.18), and *Mnemiopsis*, without tentacles. A very specialized type of ctenophore is *Cestum veneris* of the Mediterranean. In this form the body is compressed laterally and elongated to produce a thin, narrow plate, sometimes as long as 4 feet. The minute creeping ctenophores, *Coeloplana* and *Ctenoplana*, represent another extreme type in which the body is flattened and otherwise modified for a creeping existence.

Ctenophores are unfamiliar to most students. It is practically impossible to preserve them satisfactorily for examination in the laboratory, but they present many interesting features for those fortunate enough to study them alive at the seashore.

Radiata and Bilateria

As indicated in Chapter 7 (p. 221), the Coelenterata and Ctenophora constitute the grade Radiata, standing apart from and below the grade Bilateria which includes all higher Metazoa. Although roughly comparable to the coelenterates in many ways, the ctenophores have progressed in evolution to a somewhat higher level than the coelenterates, but in a direction which evidently does not lead toward the higher Metazoa.

When the classification into radiates and bilaterals is interpreted in terms of evolution, the Radiata must be regarded as a very ancient type of animal life. They show great specialization along their own lines, but the fundamental body plan, the two-layered sac surrounding a cavity with only one opening to the exterior, is remarkably simple. It may be significant from the standpoint of evolution that a similar body plan occurs as a transitional stage, the so-called gastrula, in the development of most of the higher animals.

The widespread occurrence of a hollow, two-layered stage in the ontogeny of metazoans led the great German biologist, Ernst Haeckel (1834 1919), to propose the famous **Gastraea Theory**. According to Haeckel, both radial and bilateral metazoans pass through a gastrula stage in development because they have descended, by different evolutionary pathways, from a remote common ancestor—a primitive metazoan with the general characteristics of a gastrula, which Haeckel called a gastraea. Unfortunately, it is impossible to prove or disprove phylogenetic theories; the evidence for the existence of an ancestral gastraea is of the same indirect nature as that which supports Haeckel's broader **Recapitulation Theory** (see p. 225). To many modern biologists the evidence suggests rather that the supposed common ancestor of Radiata and Bilateria was a two-layered form without an internal cavity, somewhat resembling the planula larva of coelenterates and hence referred to as a planuloid or planula-like form (cf. Fig. 7.3, p. 219). Whichever interpretation we follow, the assumption that ectoderm and endoderm are homologous in Radiata and Bilateria implies that these groups originated in a common ancestor. We turn now to a consideration of the simplest of the Bilateria, in the phyla Platyhelminthes and Nemertinea.

CHAPTER 11

THE FLATWORMS: Phyla Platyhelminthes and Nemertinea

The name flatworm, applied to members of the phyla Platyhelminthes and Nemertinea is appropriate because these animals are worm-like and are flattened dorsoventrally. The nemertineans are often considered as members of a class Nemertinea included within the phylum Platyhelminthes, but the differences between these groups justify giving the nemertines the rank of a separate phylum. In contrast to the Mesozoa, the Porifera, and the Coelenterata, the flatworms are bilaterally symmetrical animals. They show, also, anteroposterior differentiation; that is, they have "head" and "tail" ends, and they normally progress in locomotion with the head end foremost. Bilateral symmetry usually implies dorsoventral differentiation, characteristic of these worms as of the vertebrates with their "back" and "belly" surfaces.

The Phylum Platyhelminthes

The members of the phylum **Platyhelminthes** may be characterized as animals with bilateral symmetry; with a digestive cavity or enteron having a single opening, the mouth-anus; with epidermis, gastrodermis, and mesenchyme, but without a body cavity of any kind between enteron and body wall; with an excretory system of flame bulbs and ducts, called protonephridia; and with complex reproductive organs of a distinctive type. The phylum includes three classes: the class **Turbellaria**, planarians and other typically free-living flatworms; the class **Trematoda**, flukeworms; and the class

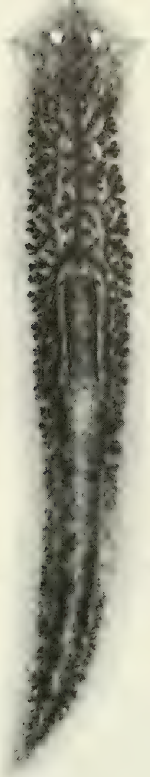


Fig. 11.1. A typical fresh-water triclad turbellarian, *Dugesia tigrina*. Note the three chief branches of the gut, each with numerous branching subdivisions. (Photograph courtesy General Biological Supply House, Inc.)

Cestoda, tapeworms. The flukes and tapeworms are widely known, at least by name, but the turbellarians, although most representative of the Platyhelminthes, are not familiar animals.

Most Turbellaria are small and inconspicuous. They live in the shallow waters of the ocean and in fresh water; some tropical species are terrestrial but are found only in humid places. A few turbellarians are parasitic upon the outer surfaces of other animals. In making comparisons between flatworms and other phyla it is necessary to use the Turbellaria alone, since the Trematoda and Cestoda are much specialized in adaptation to their parasitic existence. When the Turbellaria are thus used to represent the Platyhelminthes, the members of this phylum are seen to exhibit certain primitive features, such as a single opening to the digestive tract, and also more specialized features, such as their bilateral symmetry. They are, in fact, the simplest members of the Bilateria. The Trematoda and Cestoda are important because they present excellent examples of the structural modifications characteristic of parasites, and because they include many parasites dangerous to man and to domesticated animals.

THE CLASS TURBELLARIA

Five orders of Turbellaria are generally recognized, ranging from very simple to rather complex animals. These orders are distinguished partly by the nature and shape of the digestive tract and are descriptively named; thus

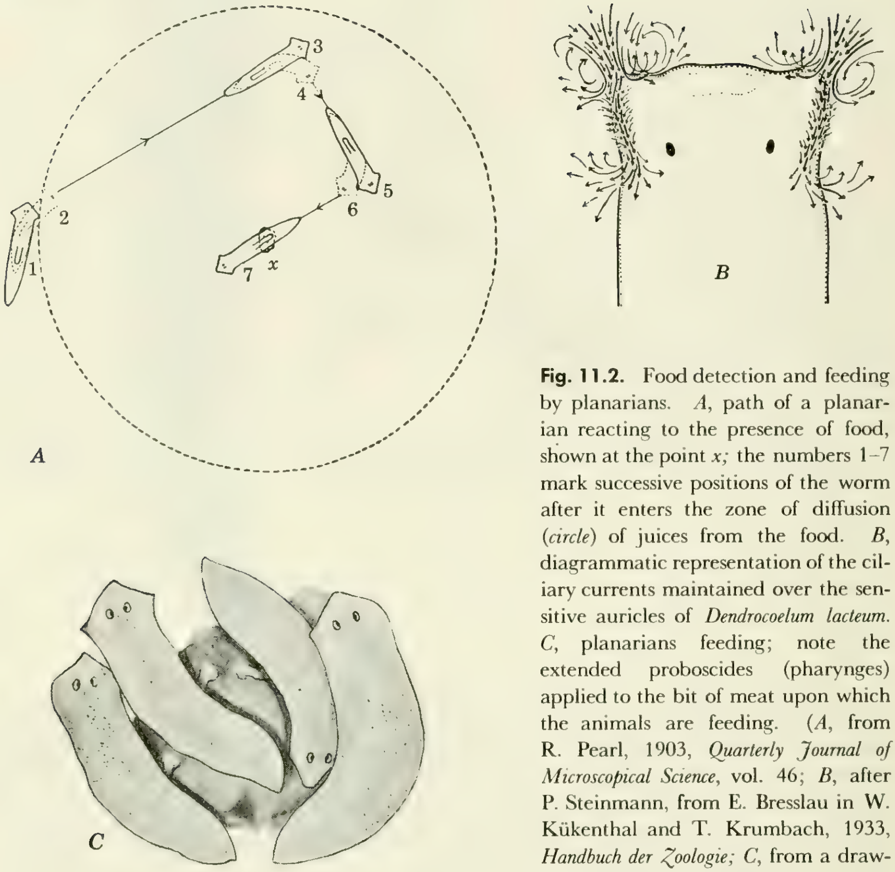


Fig. 11.2. Food detection and feeding by planarians. *A*, path of a planarian reacting to the presence of food, shown at the point *x;* the numbers 1–7 mark successive positions of the worm after it enters the zone of diffusion (*circle*) of juices from the food. *B*, diagrammatic representation of the ciliary currents maintained over the sensitive auricles of *Dendrocoelum lacteum. C*, planarians feeding; note the extended proboscides (pharynges) applied to the bit of meat upon which the animals are feeding. (*A*, from R. Pearl, 1903, *Quarterly Journal of Microscopical Science*, vol. 46; *B*, after P. Steinmann, from E. Bresslau in W. Kükenthal and T. Krumbach, 1933, *Handbuch der Zoologie; C*, from a drawing by George T. Kline.)

Acoela ("without cavity"), **Alloeocoela** ("different cavity"), **Polycladida** ("many branches"), **Tricladida** ("three branches"), and **Rhabdocoela** ("rod cavity"). The acoels and polyclads are exclusively marine; the alloeocoels are predominantly marine but are found also in brackish and fresh water; the triclads and rhabdocoels occur chiefly in fresh water. The turbellarian body is usually flattened as in most Platyhelminthes and is differentiated anteriorly into a region which may be called a head. Cilia are found upon the entire external surface of some turbellarians but usually occur only in limited areas. The name Turbellaria (*turbella*, a small whirlpool) refers to the effect produced by the action of these cilia (Figs. 11.1, 11.2). The mouth may be located in any position along the ventral midline, from the anterior to the posterior end, in different species; the usual and apparently primitive position is near the center of the body. As in coelenterates, the body is covered externally by epidermis, and the digestive cavity is lined by gastrodermis. Between these epithelial layers is a spongy meshwork of mesenchyme, in which are distributed muscle fibers, gland cells, and wandering cells. The excretory, nervous, and reproductive systems are embedded in this spongy tissue. The turbellarian is thus triploblastic, or three-layered, in contrast to such a coelenterate as the hydra, which is diploblastic.

Fresh-Water Planarians. ***Habitat, General Structure, and Activities.*** The term planarian is sometimes applied to both polyclads and triclads but usually refers to the triclads alone. Triclads are common in fresh water. Like the hydras, the planarians have long been familiar objects of study to zoologists and are well suited to illustrate the structures and functions typical of the phylum to which they belong. Such species as *Dugesia tigrina*, *D. dorotocephala*, and *Cura foremanii* are widely distributed in North America. They occur in ponds and streams, usually on the shaded sides of submerged objects. They avoid strong light and are probably nocturnal in many of their activities. In nature they feed on the bottom ooze with its microscopic plants and animals, on dead animals, and on living forms such as small mollusks and arthropods; these they capture by enfolding the prey with the margins of the body and then applying the extruded pharynx. When bits of meat are placed in a dish containing planarians not recently fed, the worms begin to move about and soon most of the individuals will be found with the pharynx attached to the food (Fig. 11.2). Species of the genera *Dendrocoelum* and *Procotyla* have a special sucker-like organ at the anterior end, by means of which they seize active prey and hold it while the pharynx attaches for feeding.

Normal, gliding locomotion is brought about by the action of the ventral and lateral cilia, beating in a layer of mucus secreted as the animal moves. A more rapid and active locomotion is effected by a variety of muscular contractions of the body.

Structures and Functions Related to Metabolism. In feeding, the muscular, tube-like **pharynx** is extruded from the mouth and attached to the food, which may be partially digested by fluid from the pharynx before it is transferred to the digestive cavity (Fig. 11.2). At rest the pharynx lies withdrawn into a sheath-like cavity; the mouth is actually the external opening into the pharynx sheath, and it is through this opening that the pharynx or proboscis is extended in feeding. Food is drawn in through the cavity within the pharynx itself and then passed into the enteron, with its three main branches and lesser subdivisions. Digestion occurs chiefly, if not entirely, within the gastrodermal cells lining the enteron; extracellular digestion is apparently limited to the preliminary softening or liquefaction of foods by the action of fluids from the pharynx. As in coelenterates, the planarian digestive cavity, extensively branched throughout the body, assumes in part the functions of a distributing system; no part of the body of the worm is far removed from a branch of the enteron. The products of digestion, as well as oxygen absorbed through the epidermis, are also distributed by way of the lymph-like fluid filling the interstices of the mesenchymal meshwork.

The **excretory system**, as it is usually called, consists of minute tubules beginning as **flame bulbs** in all parts of the mesenchymal region and uniting to form

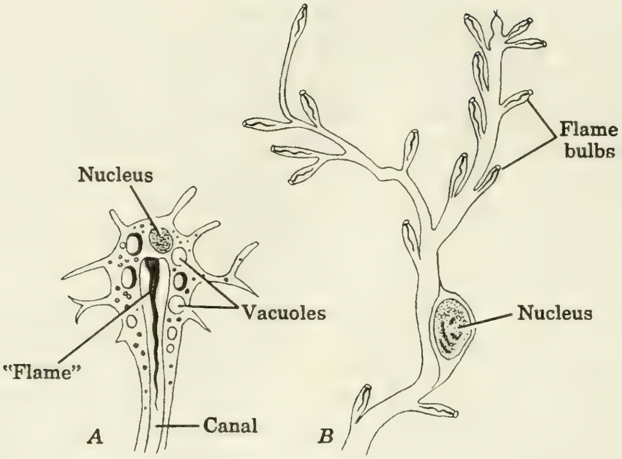


Fig. 11.3. Protonephridia of turbellarians. *A*, individual flame cell of a planarian. *B*, group of flame bulbs and their canals, with a single nucleus; from the rhabdocoel *Mesostoma*. (Redrawn, after various authors, from E. Bresslau in W. Kükenthal and T. Krumbach, 1933, *Handbuch der Zoologie*.)

larger tubes, which open to the exterior by a number of dorsolateral excretory pores. The flame bulbs, or flame cells, are so named because of the flickering tufts of cilia beating within their cavities (Fig. 11.3). These cavities are intracellular spaces and are continued as intracellular ducts within the cells making up the tubules. A system composed of these and other similar units is a distinctive feature of trematodes and cestodes, as well as of turbellarians; such systems also occur in animals belonging to other phyla. Flame bulbs are termed **protonephridia,** and any system of flame bulbs and ducts leading to external orifices is a **protonephridial system.** In ascribing an excretory function to protonephridia, it is supposed that the tufts of cilia in the flame bulbs, and other cilia lining the tubules, set up currents flowing toward the external openings. Fluids, containing metabolic wastes in solution, may presumably enter the system from the lymph by passing through the flame cells, and may be driven from the body through the excretory pores. It is probable, however, that the chief function of the protonephridia, as of protozoan contractile vacuoles, is in maintaining water balance, with excretion as an incidental process.

The Nervous System and Responsiveness. The nervous system is well developed in correlation with the complex musculature of planarians. A pair of eyes, consisting of cup-shaped groups of light-sensitive cells, is found in the dorsal surface of the head region (Fig. 11.4). Beneath the eyes lies a concentration of nervous tissue, the **brain** or **cerebral ganglia.** Two **nerve cords** extend to the posterior end of the body, and there are transverse connections between these cords throughout their length. These elements altogether constitute what may be termed a **central nervous system** (Fig. 11.5). From the

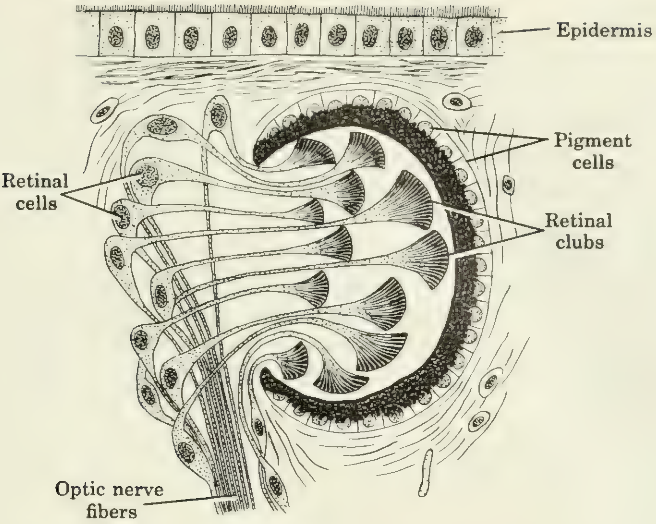
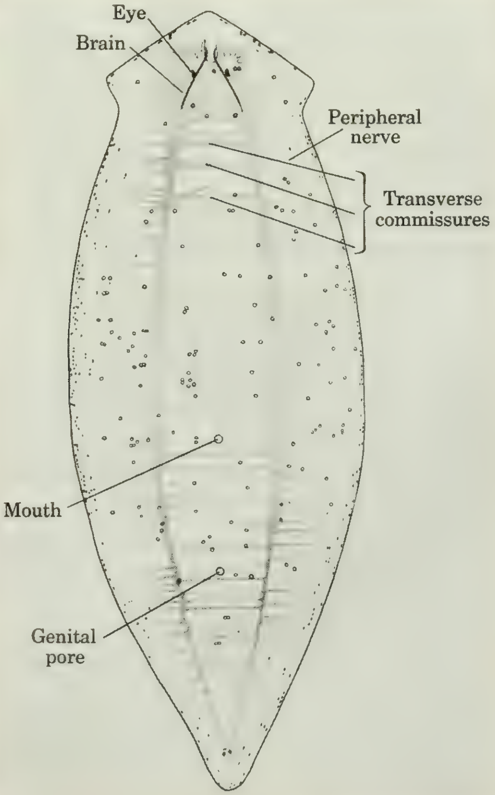

Epidermis
Pigment cells
Retinal cells
Retinal clubs
Optic nerve fibers

Fig. 11.4. The eye of a planarian in vertical section; semidiagrammatic. The midline of the body is to the right in this figure; the retinal elements are stimulated only by light rays entering the opening in the pigment cup. (Redrawn from L. von Graff, 1912, in H. G. Bronn, *Klassen und Ordnungen des Thierreichs.*)

Fig. 11.5. Major features of the nervous system of a planarian, *Planaria gonocephala.* The small dark flecks near the lateral margins represent sense organs; the small circles mark the locations of dorsal and ventral excretory pores. (From L. von Graff, 1912, in H. G. Bronn, *Klassen und Ordnungen des Thierreichs.*)


Eye
Brain
Peripheral nerve
Transverse commissures
Mouth
Genital pore

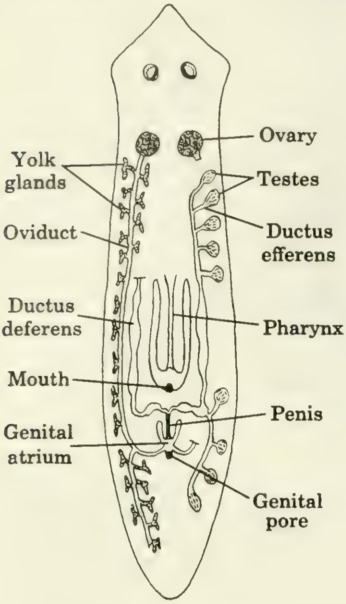


Fig. 11.6. Reproductive organs of a planarian; ventral view, diagrammatic. Parts of the female system are shown on the left, parts of the male system on the right. The copulatory bursa, which connects with the genital atrium, has been omitted for clarity.

brain and cords **nerves** extend to all parts of the body, particularly to the anterior end. **Neurons** are not easily recognizable in planarians, but they can be demonstrated in certain regions. It is assumed that the relationships of sensory, motor, and perhaps adjustor cells are comparable with those in other invertebrates that have central nervous systems. Planarians evidently have a well-organized nervous mechanism as the basis for their complex sensory and muscular reactions. At the surface of the body, in addition to the eyes, occur a variety of sensory receptor cells specialized for the reception of chemical and tactile stimuli. The structure of the eye in many planarians indicates that light from a definite direction may be an effective stimulus, as well as mere illumination; however, there seems to be no mechanism for image formation. Planarians respond to many different stimuli with a rather high degree of coordination.

The Reproductive System, Reproduction, and Development. The planarian reproductive system is complex and highly specialized. The worms are monoecious, each individual having both male and female systems (Fig. 11.6). The male system includes numerous **testes,** arranged in paired longitudinal rows. Each testis is connected by a **ductus efferens** to the longitudinal **ductus deferens** on its own side of the body. The two ductus deferentes enlarge posteriorly to form **spermiducal vesicles** in which spermatozoa are stored in advance of copulation. The spermiducal vesicles unite in the midline of the body, posterior to the pharynx sheath, and form the tubular cavity traversing the **penis,** or male copulatory organ. The penis lies in a cavity, the **male antrum,** which is just anterior to, and connects with, a second cavity, the

genital atrium. The **genital pore** opens on the ventral side of the body, posterior to the mouth, and connects the genital atrium to the exterior. The relationship of the penis to its cavity, and to the genital atrium, is similar to that of the pharynx to its sheath. During copulation, the penis is thrust from the genital pore in the same manner as the pharynx is thrust from the mouth during feeding.

The female system consists of a pair of **ovaries,** from which the ova arise, located usually just behind the head region. A single **oviduct** leads posteriorly from each ovary, receiving in its course a series of smaller ducts from the numerous **yolk glands** which surround it throughout its length. The two oviducts may unite posteriorly at the midline to form a common chamber, the **female antrum,** lying just behind the genital atrium and connected to it. In other species the paired oviducts join the genital atrium directly. Most planarians possess also a bulbous, blindly ending chamber, the **copulatory bursa,** opening either from the genital atrium or from the female antrum and extending a short distance dorsally and anteriorly.

The functional aspects of this complex system may now be considered. Sexual reproduction in planarians usually involves copulation, in which the genital pores of two worms are brought together and the penis of each worm is inserted through the genital opening and into the copulatory bursa of the other. Mutual exchange of spermatozoa from the spermiducal vesicles thus occurs, and copulation is completed by this insemination. After the partners have separated, the spermatozoa received in copulation are transferred, or move, from the copulatory bursa into the paired oviducts and finally come to rest in the anterior end of each oviduct. Here, adjacent to the ovary and separated from it by a membrane, is a **seminal receptacle,** in which spermatozoa are stored. Eggs released by the ovary break through the membrane, are fertilized, and pass down the oviduct where they are surrounded by yolk

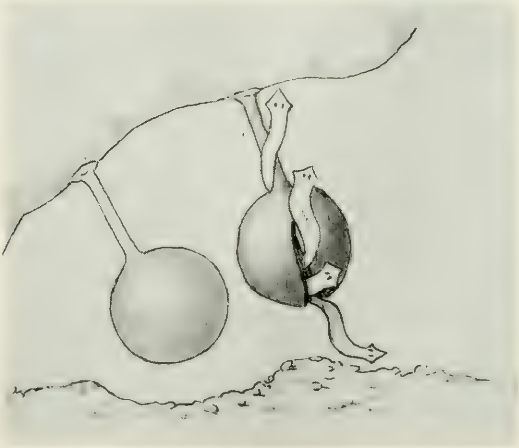


Fig. 11.7. Planarian egg capsules, or cocoons, and juvenile planarians emerging. (Drawn by George T. Kline.)

cells. The zygotes and their accompanying supplies of yolk cells are gathered in the genital atrium, where numbers of them are enclosed in a shell or cocoon secreted by numerous gland cells in the wall of the atrium. A stalk, continuous with the cocoon, is secreted through the genital opening and fastened to the substratum; as the worm creeps away, the cocoon is drawn out of the atrium and left supported by its stalk. Within the cocoon the zygotes develop into embryos which engulf the yolk cells and use their substance as food during further development. After several days or a few weeks, depending on external conditions, the cocoon ruptures, and small juvenile worms emerge (Fig. 11.7). Except for their smaller size and the absence of a reproductive system, which develops later, these juveniles resemble the adults in most respects.

Although complete male and female systems are thus present in each individual, conditions which are not well understood apparently prevent self-fertilization in most cases. Only a few species of fresh-water planarians are known to produce fertile eggs without copulation; in some of these the eggs undoubtedly develop parthenogenetically, but the possibility remains that in others the eggs may be fertilized by spermatozoa from the same worm.

In many species of planarians reproduction occurs also by **transverse fission,** usually in the post-pharyngeal region. In most of these species the worm merely constricts and so divides itself into a head- and a tailpiece, each of which heals the wound, forms the missing parts by cell division, localization, and differentiation, and undergoes regulation of proportions.

Regeneration. As may be demonstrated by a variety of experiments, many species of planarians have great powers of regeneration (Fig. 11.8). The regenerative process, by which even a small piece of the animal may form a perfect individual, involves healing of the wound surfaces and formation of a small amount of new tissue at these regions, followed by the same processes encountered in the growth of a new individual after fission. **Totipotent** or **formative cells** are apparently instrumental in regeneration; these cells have been interpreted as undifferentiated cells of the mesenchyme which move into an injured area and by repeated divisions produce the tissues required for repair. In regenerative processes even small and irregular fragments exhibit **polarity,** so that the axes of the original body are preserved in the new individual. Each piece has the capacity to form a normal adult, except in special cases in which an abnormal worm is formed—for example, an individual with two heads or two tails.

Cellular Structure and Function. The **epidermis** is composed of cuboidal or flattened cells, ciliated only in the ventral and lateral regions of the body (Fig. 11.9). The epidermal cells rest upon a thick basement membrane which functions as an elastic skeleton. Attached to the inner surface of this membrane is a mesodermal **musculature** of longitudinal, transverse, and diagonal fibers; dorsoventral fibers are also present, extending vertically between the dorsal and ventral basement membranes. The muscle fibers are cytoplasmic extensions of cells whose nuclei are inconspicuous. As previously

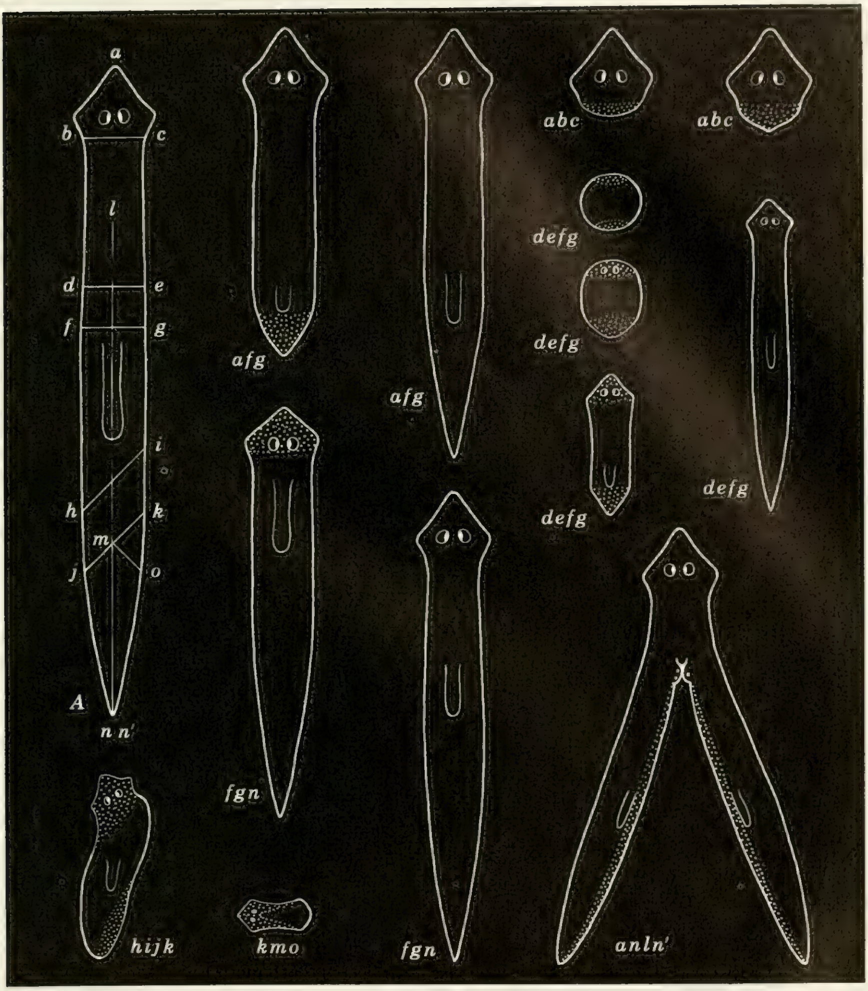


Fig. 11.8. Regeneration in planarians. The regeneration of pieces, cut from a worm along the lines marked in *A*, is shown by the labeling of the remaining figures. For example, a piece removed by cuts along lines *de* and *fg* regenerates as shown by the figures marked *defg*. Stippled areas represent portions formed as new tissue during the early stages of regeneration.

indicated, the muscles, the enteron, and the reproductive systems are surrounded by mesenchyme which fills the space within the body wall. The mesenchyme contains epidermal **gland cells** responsible for the secretion of mucus and of the bodies called **rhabdites** whose function is problematic; the gland cells open on the surface of the body. In the meshes of the mesenchyme are also found the formative cells whose role in regeneration has just been described. The relation between the mesenchyme and the excretory system has also been pointed out earlier.

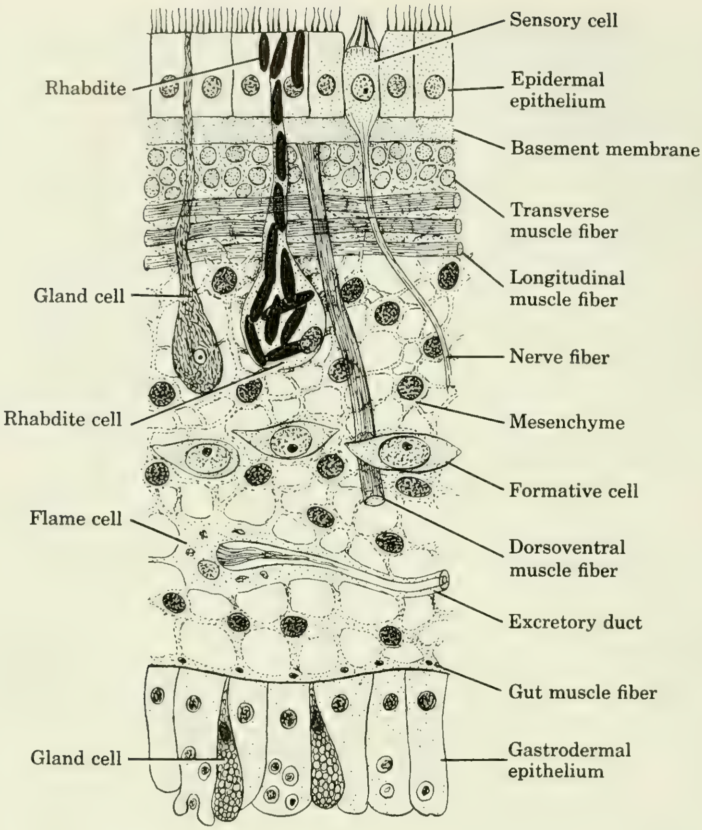

Sensory cell
Rhabdite
Epidermal epithelium
Basement membrane
Transverse muscle fiber
Gland cell
Longitudinal muscle fiber
Nerve fiber
Rhabdite cell
Mesenchyme
Formative cell
Flame cell
Dorsoventral muscle fiber
Excretory duct
Gut muscle fiber
Gland cell
Gastrodermal epithelium

Fig. 11.9. Diagrammatic representation of the cellular structure of a planarian, as seen in a longitudinal section.

The **gastrodermal cells**, of endodermal origin, line the enteron and function in digestion. It has been demonstrated that digestion occurs chiefly if not entirely in food vacuoles within these cells, and also that the gastrodermal cells store most of the food reserves.

Other Turbellaria. The foregoing account refers almost exclusively to fresh-water planarians, representatives of the order Tricladida. The marine triclads are much like those of fresh water, with the differences involving chiefly modifications of the reproductive system. The terrestrial triclads are large forms living in the upper layers of soil or upon vegetation in warm, moist, tropical habitats. In temperate climates they sometimes occur in greenhouses, into which they have been introduced, probably from the tropics.

The order Rhabdocoela, recognized by the straight, "rod-shaped" gut (Fig. 11.10), contains turbellarians, mostly of small size and thus not so favorable for study as planarians, although they are abundant in fresh water. Some have the mouth and pharynx in the middle of the ventral surface, as in

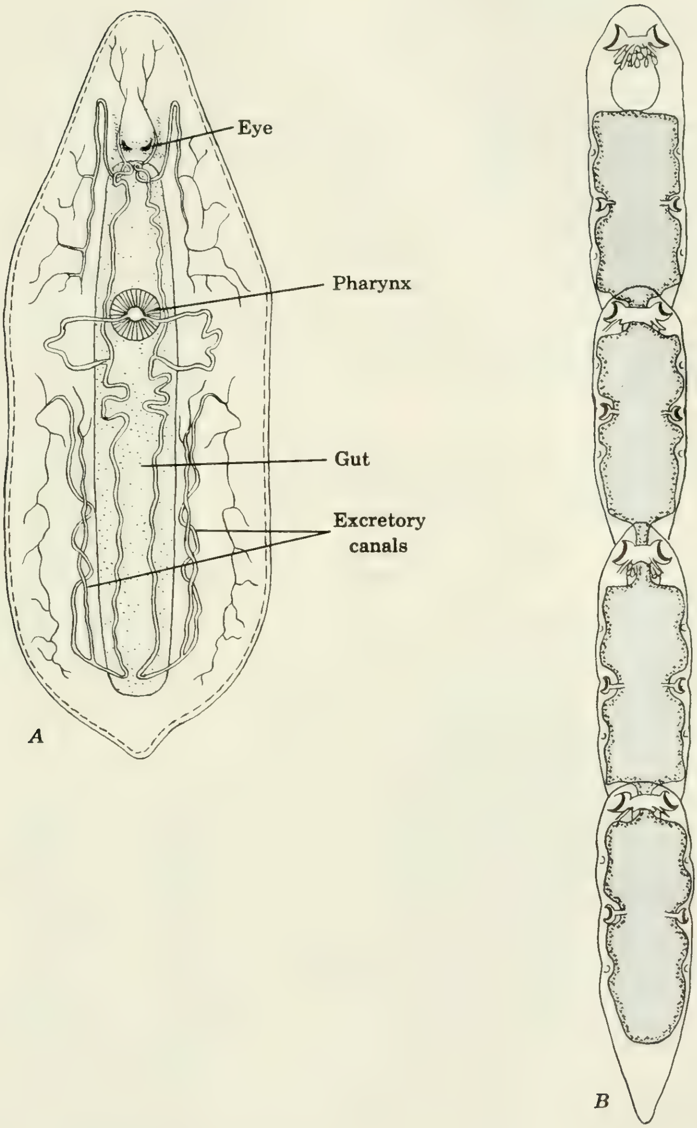


Fig. 11.10. Order Rhabdocoela. *A*, a typical rhabdocoel, *Mesostoma ehrenbergii*, showing the simple, rod-like gut and the general features of the protonephridial system. *B*, asexual reproduction in *Stenostomum grande;* each of the daughter individuals produced by the first division has undergone further division, and various stages in the formation of new heads are evident along the chain. (*A*, redrawn, after Steinmann and Bresslau, from E. Bresslau in W. Kükenthal and T. Krumbach, 1933, *Handbuch der Zoologie; B*, redrawn from E. Marcus, 1945, *Zoologie*, no. 10, University of Sao Paulo, Brazil.)

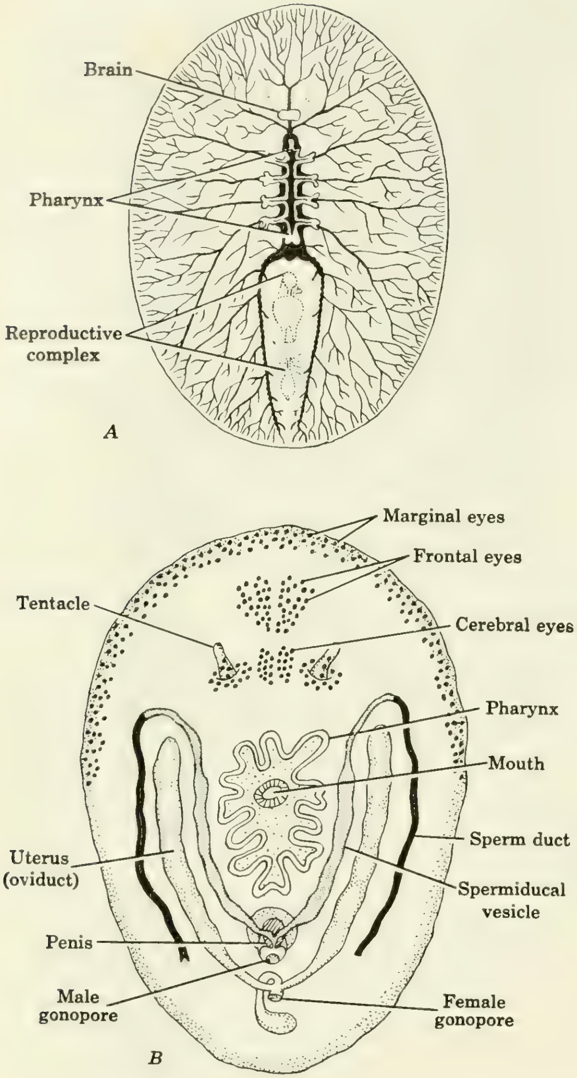

Brain
Pharynx
Reproductive complex
A
Marginal eyes
Frontal eyes
Tentacle
Cerebral eyes
Pharynx
Mouth
Sperm duct
Uterus (oviduct)
Spermiducal vesicle
Penis
Male gonopore
Female gonopore
B

Fig. 11.11. Order Polycladida. *A*, a typical polyclad, *Planocera graffi*. *B*, composite diagram showing general features of polyclads. (*A*, redrawn, after A. Lange, from E. Bresslau in W. Kükenthal and T. Krumbach, 1933, *Handbuch der Zoologie; B*, redrawn from L. H. Hyman in F. A. Brown, Jr., *et al.*, *Selected Invertebrate Types*, copyright 1950 by John Wiley and Sons, Inc., printed by permission.)

Mesostoma, but in most species the mouth is anterior. The brain lies dorsally, and from it the two principal nerve cords extend posteriorly in the ventral part of the body. The make-up and position of the nervous system in the forms with an anterior mouth are similar to those of the nervous systems in other invertebrates. The chief features are a dorsal brain, circumenteric connectives, and a pair of ventral nerve cords which may be separate or fused at the midventral line. Some rhabdocoels reproduce actively by fission, forming chains of individuals which remain together for a considerable time before they separate (Fig. 11.10).

In the order Polycladida the gut is many-branched and the body very broad and much flattened (Fig. 11.11). Polyclads are exclusively marine and are of interest chiefly because the life cycle includes a ciliated, free-swimming larval stage which becomes an adult through a process of metamorphosis.

Members of the order Acoela (Fig. 11.12) are small, plump worms, entirely marine, which represent the simplest and apparently the most primitive type of living Platyhelminthes. As implied by the name of the order, the acoels do not have an enteron. There is usually an internal aggregation of gastrodermal cells surrounded by mesenchyme; food is brought from the mouth into temporary spaces which open to accommodate it until intracellular digestion breaks it down. Most of the specializations shown by the acoels involve the reproductive system, which is often surprisingly complex; there is no excretory system. It seems reasonable to believe that the modern acoels are most like the ancient animal type from which all Platyhelminthes have evolved.

The order Alloeocoela (Fig. 11.12) contains worms which are evidently intermediate in most of their characteristics between acoels and triclads.

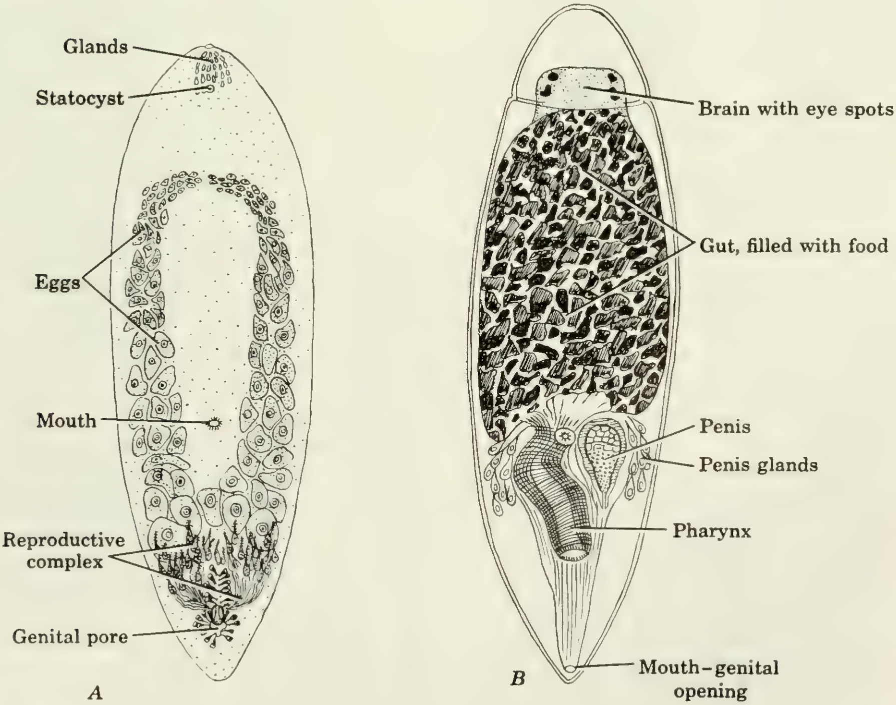

Glands
Statocyst
Eggs
Mouth
Reproductive complex
Genital pore
A
Brain with eye spots
Gut, filled with food
Penis
Penis glands
Pharynx
Mouth-genital opening
B

Fig. 11.12. *A*, order Acoela: *Anaperus gardineri*. *B*, order Alloeocoela: *Allostoma austriacum.* (Redrawn, after L. von Graff, from E. Bresslau in W. Kükenthal and T. Krumbach, 1933, *Handbuch der Zoologie*.)

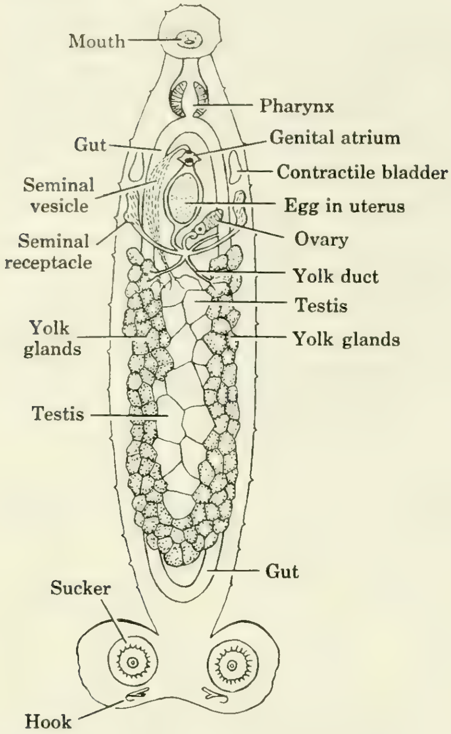

Mouth
Pharynx
Gut
Genital atrium
Contractile bladder
Seminal vesicle
Egg in uterus
Seminal receptacle
Ovary
Yolk duct
Testis
Yolk glands
Yolk glands
Testis
Gut
Sucker
Hook

Fig. 11.13. Order Monogenea; anatomy of *Sphyranura osleri*, a monogenetic trematode parasitic on external surfaces of the amphibian, *Necturus*. (Redrawn from R. R. Wright and A. B. Macallum, 1897, *Journal of Morphology*, vol. 1.)

THE CLASS TREMATODA

The class **Trematoda** includes the flukeworms, all of which are parasites. Although these worms show some structural modifications in adaptation to parasitism, notably the replacement of the epidermal layer by a cuticle and the development of hooks and suckers for attachment to the host, the trematodes have not undergone such extreme modification as the cestodes. The flattened body of trematodes is characteristic of the Platyhelminthes, and the internal structure, which includes an enteron, shows the same general relation of parts found in Turbellaria. The Trematoda are divided into the orders **Monogenea** ("one kind") and **Digenea** ("two kinds"), according to their parasitic habits and related modifications of their structure and life cycle.

Monogenea. The monogenetic trematodes are external parasites upon the body surfaces of aquatic animals, mostly vertebrates, or in cavities near the surface, such as the mouth and urinary bladder. Monogenetic parasites do not alternate between host species in the course of the life cycle. The structure of a typical monogenean is shown in Figure 11.13. In correlation with their attachment in relatively exposed positions, such trematodes have well-developed hooks and adhesive suckers. The animals are monoecious, and their reproductive organs are comparable with those of turbellarians. The eggs, which consist of a single zygote and a number of yolk cells surrounded by a shell, are laid free in the water or loosely attached to the host. A ciliated larva hatches from the egg, almost immediately attaches to the host, and transforms into a miniature adult. The life cycle is simple as compared with that of digenetic trematodes.

Digenea. The digenetic trematodes are internal parasites having at least two species of hosts in the course of the life cycle. In their adult stages, Digenea occur almost exclusively in vertebrate animals, usually infesting the blood, the urinary bladder, or the digestive tract and its appendages, the lungs and liver. Each species has its particular habitat within the host, and

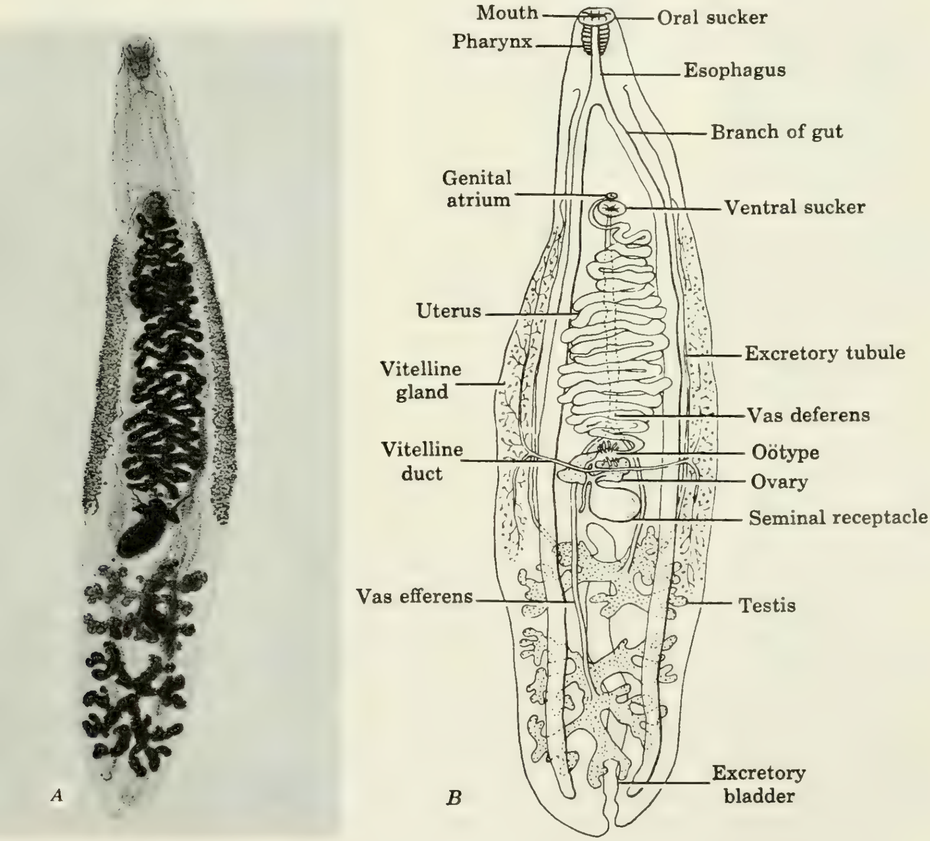

A
B
Mouth
Oral sucker
Pharynx
Esophagus
Branch of gut
Genital atrium
Ventral sucker
Uterus
Excretory tubule
Vitelline gland
Vas deferens
Vitelline duct
Oötype
Ovary
Seminal receptacle
Vas efferens
Testis
Excretory bladder

Fig. 11.14. *Clonorchis sinensis*, the Chinese liver fluke. *A*, photomicrograph of a stained and mounted specimen. *B*, diagram of a similar specimen to show the general structure. Note particularly the two large, branched testes, from which the generic name is derived, and the fact that the coiled uterus is filled with shelled eggs. (*A*, photograph courtesy Ward's Natural *Science* Establishment, Inc.; *B*, adapted from D. L. Belding, *Textbook of Clinical Parasitology*, second edition, copyright 1952 by Appleton-Century-Crofts, Inc., printed by permission.)

there is also a high degree of **host-parasite specificity**, as a result of which each stage of a particular parasite is limited to one or a few related species of host. The gut in the Digenea is typically composed of two main branches which separate from each other just behind the anteriorly placed **pharynx** and end blindly near the posterior end of the body. The nervous system is best developed in connection with the organs of attachment. The animals are monoecious, with few exceptions, and their reproductive organs are comparable, with modifications, to those of turbellarians and monogenetic trematodes.

A characteristic feature of the group is the life cycle, which is one of the most complex in the Animal Kingdom. As an example, we shall describe the life cycle of one of the Oriental liver flukes of humans, *Clonorchis sinensis* ("branched testes, living in China") (Fig. 11.14). The adult of this species is found in the bile passages of man. It produces large numbers of eggs, each of which consists of a spheroidal **shell** containing a single **zygote** and numerous **yolk cells**, like the eggs of monogenetic trematodes. These eggs pass through the bile duct into the intestine and are voided by the host in its feces. Although embryonic development is completed within the shell, the resulting larval form, the **miracidium** (Fig. 11.15), does not emerge until the egg has been ingested by a particular kind of snail. A small number of species belonging to a single family of snails are known to serve as intermediate hosts. Within the body of the snail the ciliated miracidium hatches and immediately makes its way into the tissues, where it transforms into a second larval form, the **sporocyst**. This is a thin-walled, sac-like organism which has few well-developed structural features but contains a mass of germinal tissue, from which are produced members of the next larval generation, each of which is known as a **redia** (named for the noted seventeenth-century Italian microscopist, Francesco Redi). The rediae migrate into the blood sinuses of the snail's liver, where each produces internally a group of "germ balls," each of which develops into a tailed larval stage, the **cercaria**. Several cercariae at once burst through the wall of the redia, make their way to the outside, and take up a free-swimming existence. When a cercaria encounters any one of several different kinds of fresh-water fishes, it bores through the skin, sheds its tail, and becomes encysted in the flesh of this host. This stage, consisting of the body of the cercaria which has secreted a cyst about itself and developed somewhat toward adulthood, is known as the **metacercaria**. Cysts containing viable metacercariae may be ingested by humans eating insufficiently cooked fish; in the duodenum of the final host the metacercaria emerges from its cyst and makes its way into the liver, where it soon becomes a fully matured adult and begins to produce eggs.

This life cycle, with its interesting emphasis on reproductive efficiency, may be summarized as follows: one monoecious adult, in which self-fertilization appears to be the rule, produces thousands of eggs daily over a period of years; each egg develops into **one** miracidium; each miracidium becomes **one** sporocyst; each sporocyst produces **many** rediae; each redia gives rise to **many** cercariae; each cercaria transforms into **one** metacercaria, which becomes **one**

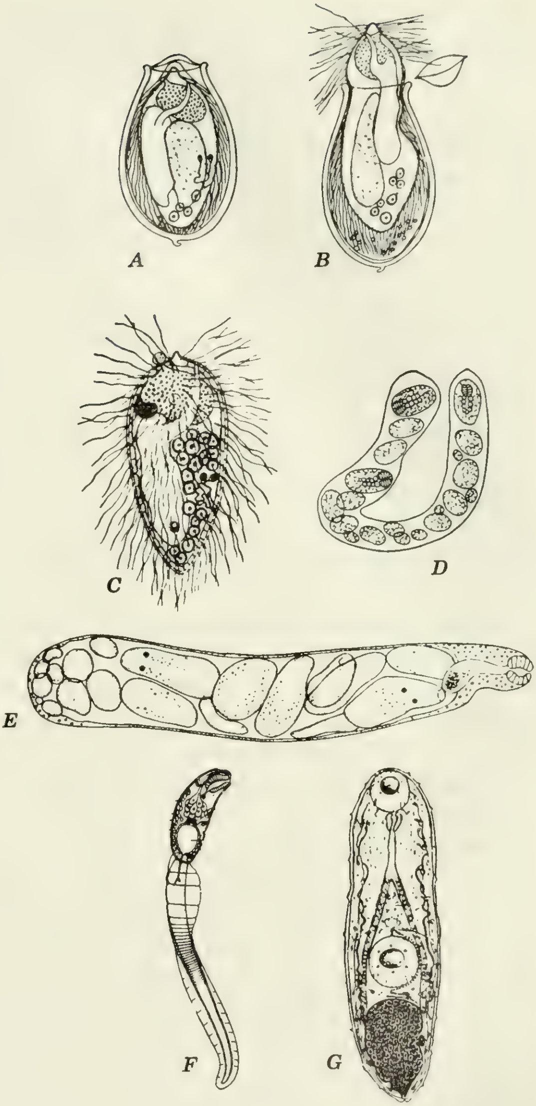


Fig. 11.15. Developmental stages of *Clonorchis sinensis*. *A*, embryonated egg, containing a well-developed miracidium. *B*, miracidium emerging from the egg capsule. *C*, miracidium. *D*, mature sporocyst from the liver of a snail, containing rediae. *E*, redia with developing cercariae. *F*, cercaria. *G*, metacercaria dissected from its cyst in the skin of a fish. *A*, *B*, and *C* are enlarged approximately ten times as much as the other figures, and *F* is somewhat more enlarged than *G*. (Adapted from D. L. Belding, *Textbook of Clinical Parasitology*, second edition, copyright 1952 by Appleton-Century-Crofts, Inc., printed by permission; *A* through *E* after Faust and Khaw, *F* after Yamaguti, *G* after Hsü and Khaw.)

adult. Thus, from each zygote, many individuals ultimately result. It must be borne in mind, however, that in order to produce the next larval generation, each stage must, within a certain time limit of survival, encounter and successfully penetrate the appropriate host. The chances **against** the survival of **all** the offspring of a single worm are astronomical, and so the species does not indefinitely increase in numbers of individuals.

The exact nature of the multiplicative processes occurring in the larval stages of digenetic trematodes has been the subject of investigation and debate for years. It is now generally agreed that the production of rediae and cercariae involves not the parthenogenetic development of eggs but rather a process somewhat resembling **polyembryony** (cf. p. 209); it might be more aptly termed **internal budding.** It is not a sexual phenomenon but an asexual one consisting of the fragmentation of a mass of germinal tissue, followed by the organization and development of each fragment into an individual of the next generation. The various intermediate stages may be interpreted as persistent larval forms which mature only to the extent of carrying on these reproductive processes.

The life cycles of other digenetic trematodes differ from that of *Clonorchis* in details only. In some the miracidium is a free-swimming larva which actively penetrates the body of the snail. In others there is more than one redial generation within the liver of the snail, or the sporocyst may produce cercariae directly without the intervention of rediae. The place of encystment of the metacercaria varies also between species; some encyst upon vegetation, where they may be readily ingested by final hosts which are herbivorous. In the blood flukes, such as those of the genus *Schistosoma*, the cercaria actually penetrates the skin of the final host and thus reaches its definitive situation in the blood vessels; there is no second intermediate host, and no metacercaria. Finally, the most complicated of the trematode life cycles is that of the genus *Alaria*, found as adults in various carnivorous mammals. This fluke requires three intermediate hosts for its successful transfer; a snail, an amphibian, and a small carnivorous mammal are all involved in this cycle before the fluke can reach the large carnivore which is its final host.

Certain genera of flukes, such as *Paragonimus*, a lung fluke of carnivorous vertebrates, and *Schistosoma*, the blood fluke, with species in Egypt, the West Indies, and the Japan-Philippines area, are dangerous human parasites. The United States has no widespread human infestations of this sort, although there is always the danger that such parasites may be introduced by persons infested in other parts of the world. The establishment of such a parasite in a new country, however, would also require the establishment of its intermediate hosts in the same area, or the adaptation of the life cycle to involve a local group of hosts. The complicated life cycles of the digenetic trematodes, together with their host specificity, thus make it difficult for them to become widespread in the absence of the proper intermediate hosts. Knowledge of the host relationships of flukes has made it posssible to take intelligent steps toward their control, including the introduction of sanitary measures and of measures for the control of the intermediate hosts.

THE CLASS CESTODA

The tapeworms, members of the class Cestoda, are familiar parasites, although infestations of man and domestic animals are now less common than they were before the life cycles of tapeworms became known and preventive measures could be taken. A representative tapeworm with its segments and radially symmetrical anterior organ of attachment has little resemblance to other flatworms, but examination reveals homologies that clearly place these worms with the trematodes and the turbellarians. The structure of the cestode is, however, more specialized in relation to parasitism than is the structure of the trematode, when each is compared with the free-living turbellarians. Not only is the epidermal layer lacking, as in the majority of trematodes, but the cestode has no digestive tract and no endoderm cells, even in its development. The reproductive and excretory systems establish the relationship, however, since these parts are unique and fundamentally like those of other Platyhelminthes. The apparent dissimilarity between the non-segmented fluke or planarian, on the one hand, and the segmented tapeworm, on the other, is not so important as it might seem. Segmentation does not occur in the cestode subclass **Cestodaria**; and in the subclass **Eucestoda** there are some species in which segmentation is lacking or little developed. The segmentation is in fact only a reduplication of the part of the individual containing the reproductive organs and is not entirely comparable with the segmentation of such a truly metameric form as the earthworm. The segmentation of the tapeworm may be regarded simply as a device for increasing the reproductive potential.

The Subclass Cestodaria. These non-segmented tapeworms have an organ of attachment resembling the head-like **scolex** of the Eucestoda, but they lack the segments, or **proglottids**, of the true tapeworms, and they have only one set of reproductive organs instead of many sets (Fig. 11.16). Like the Eucestoda, they are covered by a cuticle instead of an epidermis, and they have no mouth or digestive tract. A characteristic ten-hooked larval stage is present in the life cycle. These worms have been compared with trematodes minus a digestive tract, and it has been suggested that they may represent an intermediate stage in the evolution of tapeworms from flukes. From several lines of evidence it now appears that the trematodes and cestodes probably had an independent origin from some free-living group, rather than that the trematodes gave rise to the cestodes. The cestodarians may, in fact, represent an early stage in the evolution of the Eucestoda; alternatively, they might be considered as degenerate eucestodes.

The Subclass Eucestoda. This subclass includes the great majority of tapeworms. The individual consists of a **scolex**, which bears the organs of attachment such as suckers and hooks; and of a segmented body, or **strobila**, composed of varying numbers of **proglottids** (Fig. 11.17). The adult animal lives in the intestine of its host, attached by the scolex and with the strobila extending into the intestinal cavity. The firm hold of the scolex enables the parasite to maintain its position despite the movement of food along the host's intestine. Adult tapeworms vary in size from such tiny forms as *Echinococcus granulosus*, which when fully mature is only a few millimeters long and consists of a scolex with four proglottids, to others such as *Taenia saginata*, which may be 4 to 10 yards in length and have thousands of proglottids. With very few exceptions, all adult tapeworms are

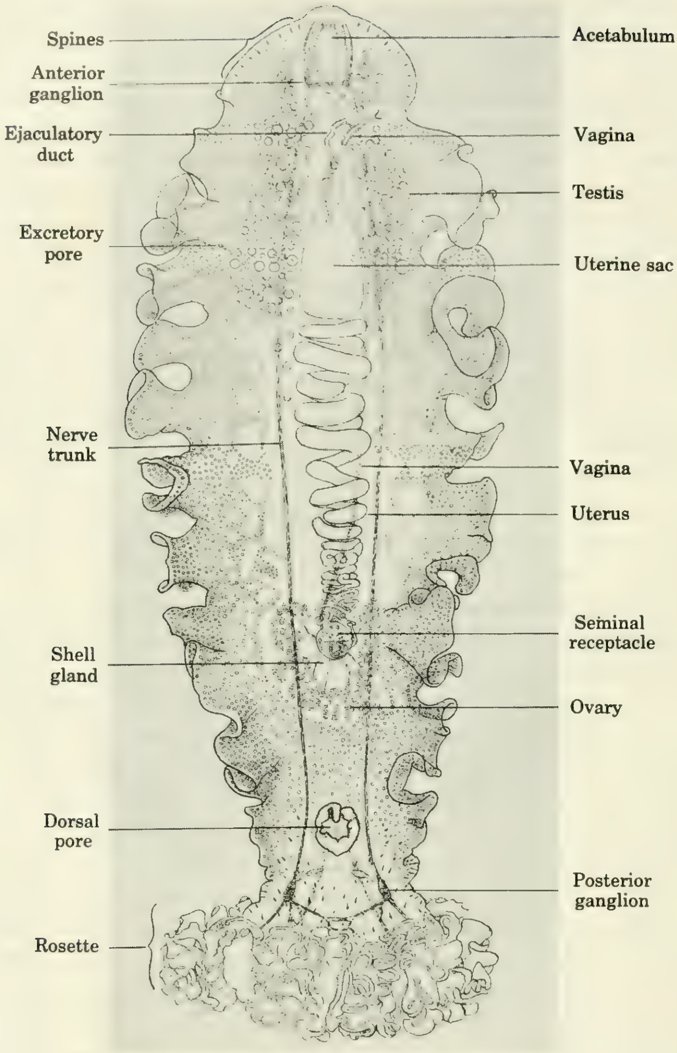

Spines
Anterior ganglion
Ejaculatory duct
Excretory pore
Nerve trunk
Shell gland
Dorsal pore
Rosette
Acetabulum
Vagina
Testis
Uterine sac
Vagina
Uterus
Seminal receptacle
Ovary
Posterior ganglion

Fig. 11.16. A typical cestodarian, *Gyrocotyle fimbriata*, from the intestine of the ratfish. (Reproduced from J. E. Lynch, 1945, *Journal of Parasitology*, vol. 31, printed by permission.)

intestinal parasites in vertebrate hosts, and their larval stages are parasites in the bodies of animals upon which the final host feeds, or which are likely to be ingested by the final host with its food. The intermediate host is infected by eggs and embryos from the feces of the final host.

The structure and life cycle of the pork tapeworm, *Taenia solium*, which infests man, is representative of a large order of tapeworms. Infestation by this species is still common in countries where raw or imperfectly cooked pork is eaten. The structure is similar to that of *Taenia saginata*, the beef tapeworm, and that of *Taenia pisiformis*, which is common in dogs wherever dogs prey upon wild rabbits. The scolex in this genus bears four suckers and is surmounted by a crown of hooks, the so-called **rostellum.** Behind the scolex is a budding zone where the proglottids originate. As new ones are formed, the older ones become farther removed from the scolex and finally detach, either singly or in short chains, from the free end of the worm, to pass out of the host with its feces.

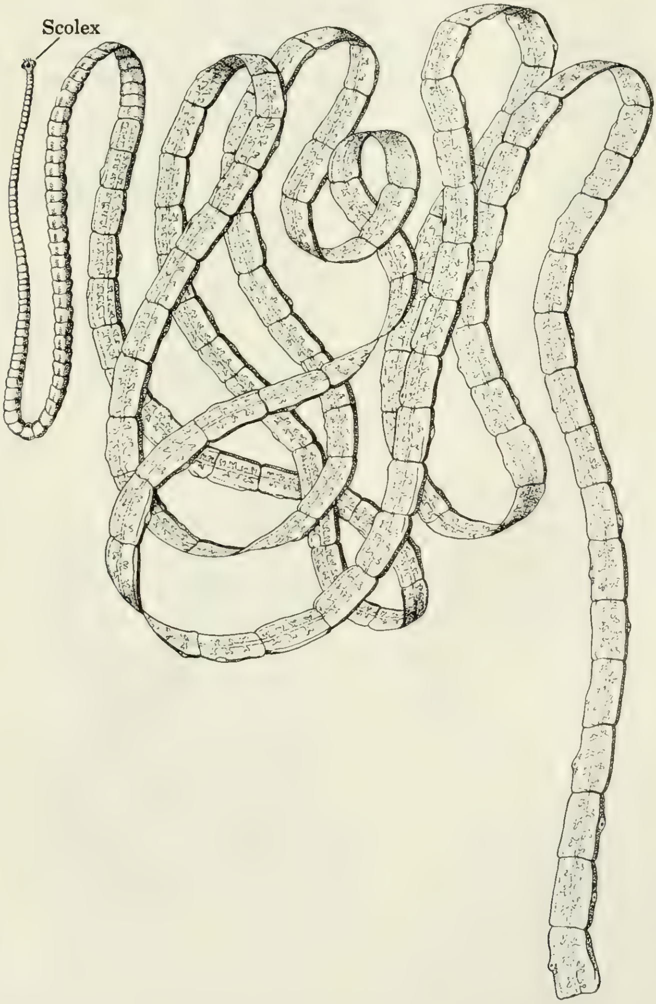


Fig. 11.17. Adult taenioid tapeworm. (Redrawn from K. von Frisch, 1953, *Biologie*, vol. 2, by permission of Bayerischer Schulbuch-Verlag.)

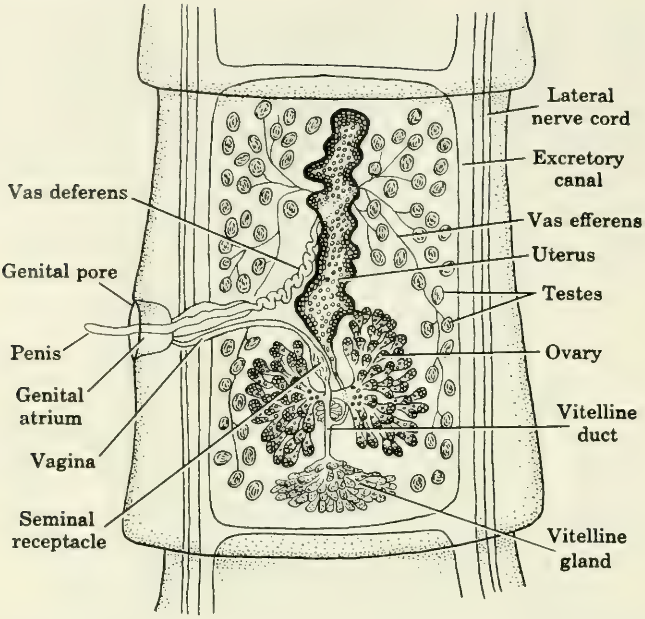


Fig. 11.18. Mature proglottid of a tapeworm, *Taenia pisiformis*, showing details of male and female reproductive systems. Note that there is no uterine pore; fertilized eggs accumulate in the enlarging uterus and are released only by rupture of the shed proglottid. (Redrawn from C. G. Goodchild in F. A. Brown, Jr., *et al.*, *Selected Invertebrate Types*, copyright 1950 by John Wiley and Sons, Inc., printed by permission.)

The internal structure of such a tapeworm is relatively simple, except for the reproductive organs. There is no mouth or digestive system; digested food in the host's intestine is apparently absorbed through the body wall of the parasite. A protonephridial **excretory system** is present, consisting of flame bulbs and ducts leading to longitudinal vessels which extend throughout the length of the body. The **nervous system** is little developed except in the scolex; a pair of longitudinal nerve trunks lying near the excretory trunks also extend throughout the length of the strobila. Sense organs and sensory cells are virtually unknown in such tapeworms, although the animal may, by movements of the scolex and contractions of the body, respond to external stimulation. This degeneration of structures important in free-living animals is common in parasites. The **reproductive system** is complex, and a complete system of male and female organs develops in every proglottid. In *T. solium* fully differentiated reproductive systems may be seen in the region from the two-hundredth to the three-hundredth proglottid. Each of these reproductive systems is comparable with the single set of male and female reproductive organs found in a turbellarian or a trematode (Fig. 11.18). The egg is likewise comparable, consisting of a **shell** enclosing a **zygote** and **yolk cells.** Self-fertilization is probably the most common means of insemination in these worms; the copulatory organ may be inserted into the vagina of the same proglottid, or into the vagina of a different proglottid in the same strobila if the worm is folded upon itself. Cross-fertilization may occur during similar contact if two or more worms are living in the same host. As the cells composing the ovaries, testes, and yolk glands in each proglottid are utilized, the eggs thus formed accumulate in the uterus, which grows as the other parts of the system dwindle. Eventually the greater part of the proglottid is occupied by the branching uterus containing tens of thousands of eggs enclosing **six-hooked embryos**, which have developed from the zygotes (Fig. 11.19). The ripe proglottids become detached, pass out of the host with the feces, and disintegrate. The embryos may thus be liberated on the surface of the ground, where they can survive protected by the shell for months and may be distributed widely like encysted protozoans.

Within the eggshell, development proceeds no further than the six-hooked embryo (hexacanth) stage unless the egg is ingested by another host; in the

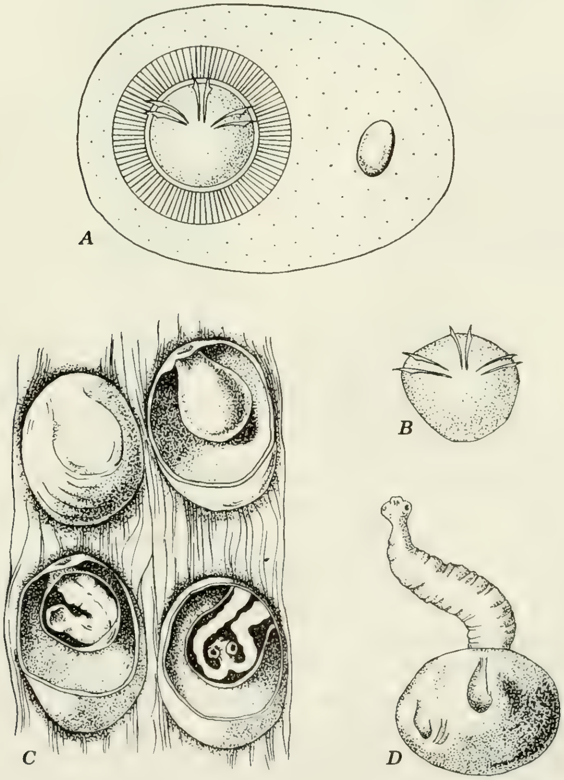


Fig. 11.19. Stages in the life cycle of *Taenia solium*. *A*, egg containing hexacanth embryo. *B*, hexacanth after emergence in gut of intermediate host. *C*, four cysticerci in pork, progressively dissected to show cyst wall, inner envelope, and invaginated scolex. *D*, cysticercus evaginating in gut of final host. (Redrawn from W. Stempell, 1926, *Zoologie im Grundriss*.)

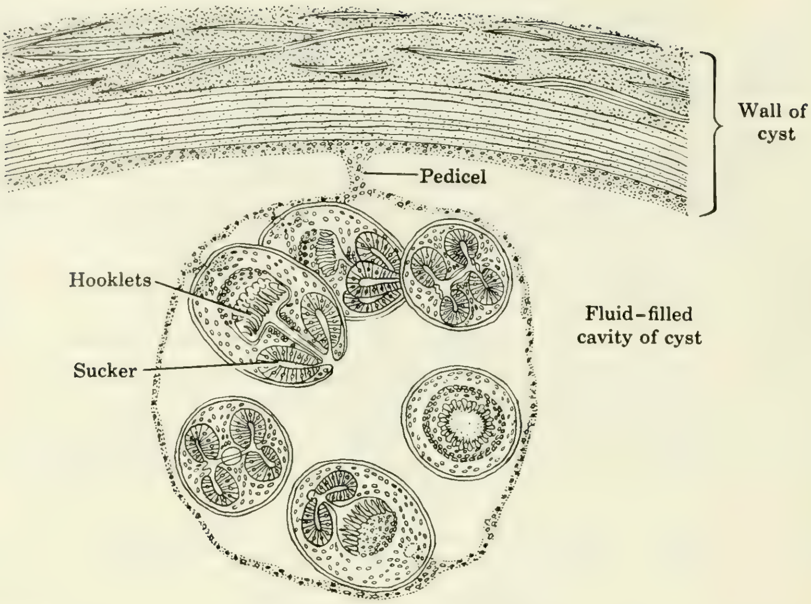


Fig. 11.20. Portion of a hydatid cyst of *Echinococcus granulosus*. The outer part of the cyst wall is produced by connective tissues of the host; the inner part is a thin syncytium from which many brood capsules, like the one shown here, arise by budding. Thousands of scoleces, each capable of producing a mature tapeworm, are formed asexually within such capsules in a hydatid cyst. (Redrawn from C. G. Goodchild in F. A. Brown, Jr., *et al.*, *Selected Invertebrate Types*, copyright 1950 by John Wiley and Sons, Inc., printed by permission.)

case of *T. solium*, this would be the pig. Within the intestine of the proper intermediate host, the eggshell is digested, but the hexacanth survives and works its way, using its hooks, through the mucous membrane and into the blood vessels or lymph channels. It may then be carried to the muscles of the host, where it develops into a form called the **bladder worm** or **cysticercus;** this stage consists of a bladder with the scolex and neck of the future adult invaginated from one point on the surface (Fig. 11.19). This bladder worm cannot develop further unless it is eaten by the final host, which in this case is man. Once in the human digestive tract, the scolex is freed by the digestion of the cyst and bladder; it then everts, attaches to the intestinal wall, begins a rapid formation of proglottids, and so produces the adult worm. Such an adult may live for some years, forming and detaching thousands of proglottids, each containing countless eggs.

This life cycle may be summarized as follows: one proglottid produces thousands of zygotes; each zygote develops into **one** hexacanth; each hexacanth becomes **one** cysticercus, which transforms into **one** adult. Thus the reproductive potential of these tapeworms is increased by multiplying the number of zygotes produced, and not, as in the Digenea, by modifications

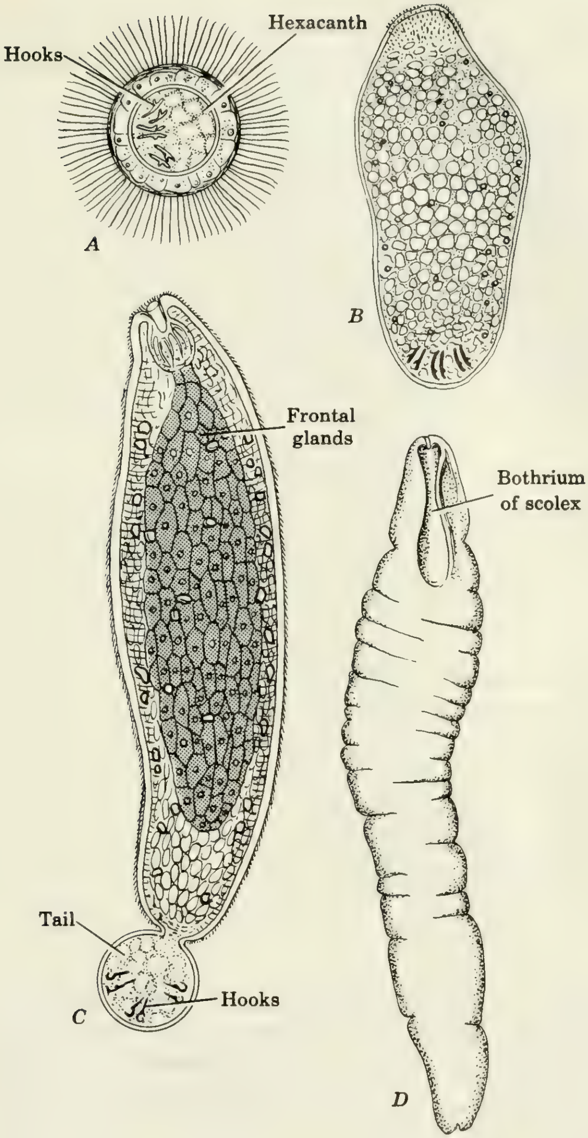


Fig. 11.21. Immature stages in the life cycle of the broad tapeworm or fish tapeworm, *Diphyllobothrium latum*. *A*, free-swimming, ciliated coracidium larvae, which is ingested by a small crustacean such as *Cyclops*. *B*, immature, and *C*, mature procercoid, developing from the hexacanth in the body of the crustacean. *D*, plerocercoid, which develops in muscles, liver, spleen, or coelom of a fish which has eaten an infected *Cyclops*. The plerocercoid transforms into the mature, segmented tapeworm in the intestine of the final host, a fish-eating mammal, after being ingested. (Redrawn, after Rosen, from L. H. Hyman, *The Invertebrates: Platyhelminthes and Rhynchocoela*, copyright 1951 by McGraw-Hill Book Co., Inc., printed by permission.)

which enable each zygote, through multiplicative larval stages, to develop into numerous adults. A step in this direction, however, is seen in the life cycle of *Echinococcus granulosus*, which is found as a minute adult in dogs, and as a larva in cattle, sheep, swine, and occasionally man. The hexacanth larvae of this worm, once they have gained access to the tissues of an intermediate host, transform into bladder worms. The originally single inverted scolex in each of these cysticerci proliferates asexually to produce thousands of daughter cysts, attached to the inner wall of the parent bladder or floating free in its fluid contents (Fig. 11.20). The cyst slowly enlarges, growing in the course of years to the size of an orange or larger. It may, if it lies in the brain, for example, bring about serious consequences to the intermediate host. From the standpoint of the parasite the advantage lies in the fact that the final host, feeding upon the flesh of an intermediate host containing one of these huge cysts, will receive a massive infestation of potential adult tapeworms.

The taenioid tapeworms which have been used as examples above represent only one, and probably the most highly specialized, of several orders of Eucestoda. Parasites dangerous to man are also found in other orders, in which the life cycles and morphology of the tapeworms differ from those of the taenioids. An example is *Diphyllobothrium latum*, the broad tapeworm of man and other carnivores. This worm possesses in each proglottid a **uterine pore** in addition to the genital pore. Through this uterine opening eggs are emitted singly as they mature, instead of reaching the outside through the shedding of entire proglottids. The life cycle of *Diphyllobothrium* (Fig. 11.21) requires for its completion a small crustacean, such as *Cyclops*, and a fish, as intermediate hosts. The stages infective for the final host are **plerocercoids,** encysted in the flesh, and particularly in the livers, of infected fish. A bear, a fox, a dog, or a man may become infested by eating raw fish. Records of massive infestations with tapeworms of this species have been obtained among fisherfolk in the Baltic area, who are accustomed to eating raw fish liver spread on bread.

Tapeworm infestations are now comparatively rare among adult human beings in communities where sanitary precautions are practiced. Meat inspection, cold storage, proper cookery, and widespread knowledge regarding modes of infection have almost eliminated *Taenia solium* and *T. saginata* as serious problems for the United States and Western Europe. This is in contrast to conditions prevailing before about 1850, when the life cycles of these parasites, and hence the means of preventing infestation, became known.

The Phylum Nemertinea

Members of the phylum **Nemertinea** are sometimes called "ribbon worms" because the bodies of many of them are greatly elongated and flattened. Most species are marine, although a few fresh-water and terrestrial nemer-

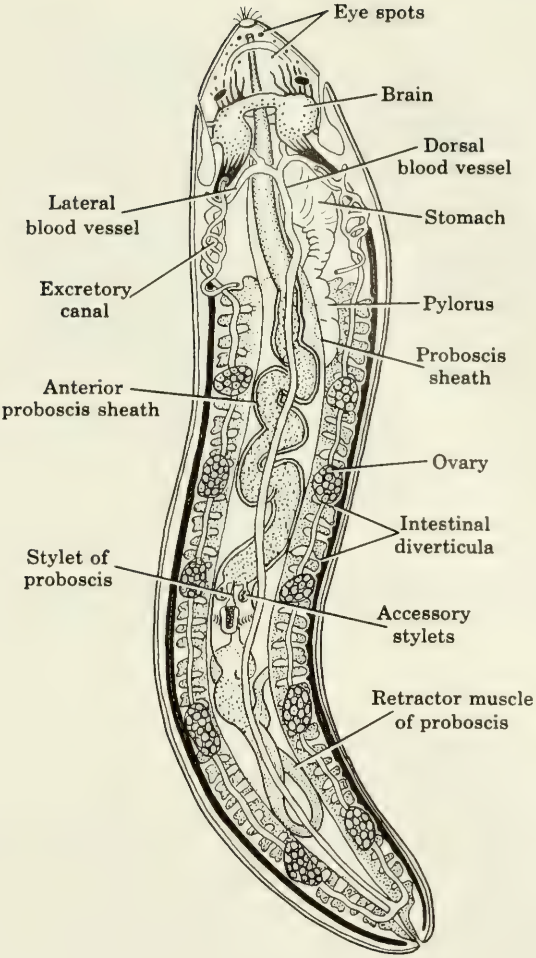

Eye spots
Brain
Dorsal blood vessel
Lateral blood vessel
Stomach
Excretory canal
Pylorus
Proboscis sheath
Anterior proboscis sheath
Ovary
Intestinal diverticula
Stylet of proboscis
Accessory stylets
Retractor muscle of proboscis

Fig. 11.22. General features of a typical nemertine, *Amphiporus pulcher;* this is a dorsal view of a female individual. The stylet is so placed that it occupies the tip of the proboscis when this is fully everted. Note the relatively simple reproductive system, consisting of a series of pouch-like ovaries, each with a separate external opening, and the longitudinal vessels of the primitive blood-vascular system. (Redrawn, after Bürger, from C. G. Goodchild in F. A. Brown, Jr., *et al.*, *Selected Invertebrate Types*, copyright 1950 by John Wiley and Sons, Inc., printed by permission.)

tines are known. Some of the marine forms are free-swimming (pelagic), but for the most part they live burrowing in the bottom or among the growths of animal and plant life of the ocean floor. One species lives as a commensal within the mantle cavities of bivalve mollusks. Common American forms are *Cerebratulus lacteus*, a burrowing species which may be several feet in length, and *Tetrastemma elegans*, less than an inch long.

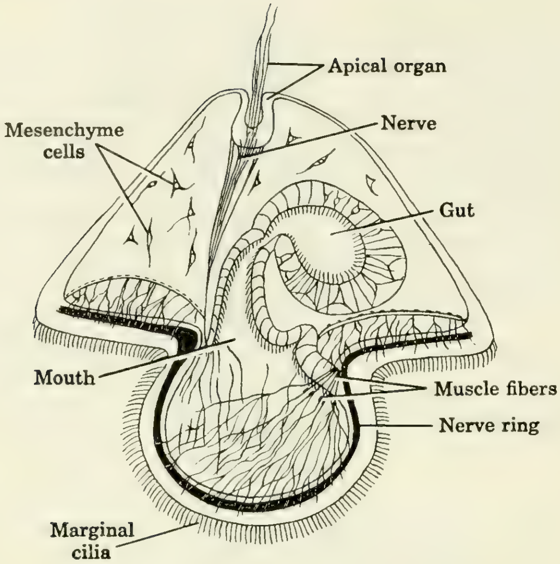


Fig. 11.23. Pilidium larva of a nemertine; optical section, showing distribution of nerve and muscle fibers. (Redrawn from W. Salensky, 1886, *Zeitschrift für wissenschaftliche Zoologie*, vol. 43.)

The structure of a representative nemertine is shown in Figure 11.22. The ciliated body is somewhat flattened dorsoventrally, with a mouth at the anterior end and an anus at the posterior end. A protrusible structure called the **proboscis**, lying in a sheath dorsal to the digestive system, is used as a tactile organ and in some species for the capture of prey. Unlike the proboscis of planarians, which is actually the pharynx, the proboscis of the nemertines is not an integral part of the digestive system, although in some types its cavity opens into the mouth. Food captured by the proboscis is brought to the mouth and ingested, and the proboscis is then retracted into its own dorsal sheath.

The alimentary canal in nemertines is a straight tube, leading from mouth to anus, usually with paired lateral pouches. The space between the internal organs is occupied by mesenchymal tissue similar to that of turbellarians; hence there is no coelomic cavity. The excretory system consists of protonephridia resembling those of Platyhelminthes but more specialized. A notable advance characteristic of nemertines is the presence of a blood-vascular system. This consists of a median dorsal vessel, and on each side a lateral longitudinal vessel. These unite at each end of the body. The blood plasma and blood cells are usually colorless. The nervous system consists of two pairs of ganglia, constituting the "brain," lying anteriorly and dorsally, and three longitudinal cords. Two cords are lateral and one dorsal, and they are connected at various levels by commissures. A number of differentiated sense organs are present, such as the eyes of some species, and special regions of sensory epithelium.

The reproductive system consists of paired, sac-like ovaries or testes lying between the lateral pouches of the digestive tract. Each gonad opens externally by a separate pore. Some nemertines are monoecious, but in most species the sexes are separate. According to the species, fertilization may occur within the body of the female or in the open water after the discharge of ova and spermatozoa. Development usually includes a ciliated, free-swimming larva, the **pilidium** (Fig. 11.23), which later metamorphoses to form the adult. In a few species the young develop into miniature adults within the body of the parent.

The Nemertinea are thus bilateral, triploblastic animals without a body cavity and with protonephridial excretory organs. To this extent they resemble the Platyhelminthes. On the other hand, they have an anal opening, a blood-vascular system, a more highly developed nervous system, and a unique feature, the proboscis. Considering also the fact that the course of embryonic development differs in the two groups, their separation into two phyla seems completely justified. These phyla can be placed together in the series Acoelomata as animals which are triploblastic and bilaterally symmetrical but lack a body cavity (see Fig. 7.4, p. 221).

The Flatworm Body Plan

As compared with any member of the phylum Platyhelminthes, the Nemertinea are obviously more highly specialized in a number of ways. The nemertines may be thought of as the culmination of evolution within the acoelomate line; as specialized end forms, they are not of particular significance in considering the typical flatworm plan. Most of the Platyhelminthes are also highly specialized types, having been modified extensively through long periods of parasitic existence. For comparative purposes, as stated earlier, the free-living Turbellaria are most significant. Their plan of organization shows an animal which is triploblastic, with epidermis, gastrodermis, and intervening mesenchyme, in contrast to the diploblastic organization of the simplest coelenterates. The dorsoventral differentiation, the anteroposterior differentiation with its correlated bilateral symmetry and development of a head, the sensory-neuro-muscular system, and the reproductive system with its complex parts are all evidences of greater specialization than anything found in coelenterates. The turbellarian can be compared with a coelenterate such as a medusa, or a shortened polyp creeping upon its oral surface, but the more obvious comparisons are with higher animals. The great diversity of forms characteristic of the series Acoelomata presents evidence of the plasticity or adaptability of this type of construction. The fact that all higher animals possess some kind of a body cavity, however, indicates that the solid-bodied construction of acoelomates has imposed limits upon evolutionary progress.

CHAPTER 12

SOME PSEUDOCOELOMATE ANIMALS AND MINOR EUCOELOMATE PHYLA

The animals considered in this chapter are structurally much more advanced than the flatworms. Perhaps the most significant feature of their particular level of organization is the presence of a body cavity between the gut wall and the body wall. Some kind of body cavity is present in all the higher animals, although in different forms it is variously developed and arises in different ways (pp. 222–223). In one small group of phyla the body cavity represents a development of the embryonic blastocoel and is not lined by a mesodermal peritoneum. Such a cavity is termed a **pseudocoel**, and animals possessing this kind of a body cavity may be grouped together as the series Pseudocoelomata (Fig. 7.4, p. 221). Of the three phyla constituting this series, we shall consider in detail only the phylum **Aschelminthes**, referring more briefly to the phyla **Acanthocephala** and **Entoprocta**.

The other phyla to be discussed in this chapter are of a different grade of construction. They have a body cavity which is a true coelom, and their affinities lie with the more advanced major phyla which will be considered in subsequent chapters. The phyla **Ectoprocta**, **Brachiopoda**, and **Chaetognatha** are called minor phyla because they consist of relatively small numbers of species. They are discussed together in this chapter not because they form a coherent, interrelated group, but because it is impossible to state with any certainty where they should be placed, in relation to the larger groups, in the phylogenetic scheme of the Metazoa.

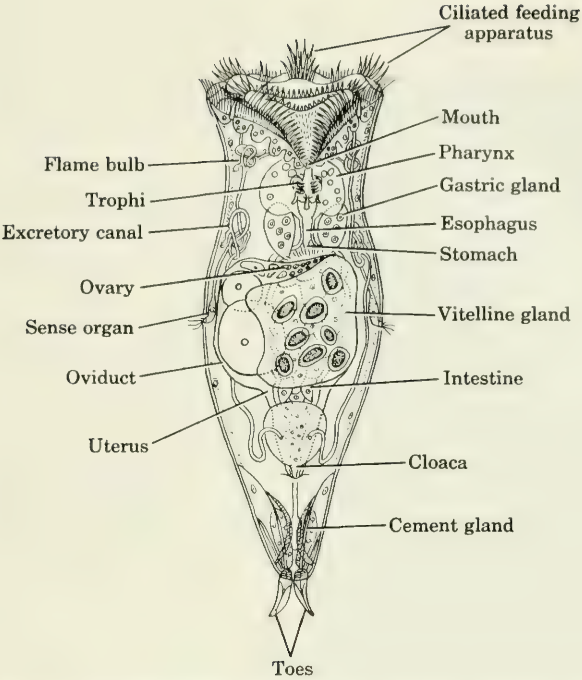

Ciliated feeding apparatus
Mouth
Flame bulb
Pharynx
Trophi
Gastric gland
Excretory canal
Esophagus
Stomach
Ovary
Vitelline gland
Sense organ
Oviduct
Intestine
Uterus
Cloaca
Cement gland
Toes

Fig. 12.1. Class Rotifera. A typical rotifer, *Epiphanes senta;* semidiagrammatic. This is a ventral view of a mature female. (Redrawn, after various authors, from C. G. Goodchild in F. A. Brown, Jr., *et al.*, *Selected Invertebrate Types*, copyright 1950 by John Wiley and Sons, Inc., printed by permission.)

Pseudocoelomate Groups

THE PHYLUM ASCHELMINTHES

The phylum **Aschelminthes** includes by all standards a mixed assemblage of widely different forms. It is composed of six classes, of which the most significant are the class **Rotifera**, or rotifers, and the class **Nematoda**, which includes the most familiar examples of the so-called roundworms. The remaining groups are of such minor importance to the general student that they need not be considered here.

The Class Rotifera. The name Rotifera, or "wheel-bearers," is derived from observations of these tiny animals by early microscopists, notably Leeuwenhoek, who in 1703 described the form as bearing "two wheels thick set with teeth as the wheel of a watch." This is particularly descriptive of many species with anterior ciliated crowns; in the feeding activities of these animals the cilia beat toward the mouth from both sides, and under low magnification the cilia give the entirely erroneous impression of two tiny wheels revolving in opposite directions. Rotifers are abundant in fresh water, and there are also many marine species. All are microscopic in size, the largest being about a millimeter in length. Rotifers are commonly free-swimming animals, but they may become temporarily attached to the substratum by secretions of their posterior adhesive glands. Many species are permanently attached, and a few live in tubes constructed of various materials and immovably fixed to the substratum.

Although there is no single species of rotifer that may be called "typical," a generalized diagram is helpful in understanding the structural characteristics of the group (Fig. 12.1). The animal is bilaterally symmetrical, and its body may be divided into **head, trunk,** and **tail** regions. It is covered by a non-living, proteinaceous cuticle secreted by the epidermis and firm enough to maintain the characteristic shape of the body. A variously specialized anterior region bears, in many species, the powerful cilia which in these forms are responsible for food-getting, and in part for locomotion. Water currents set up by the beating of these cilia converge upon the anteroventral **mouth,** carrying with them microorganisms and particles of debris upon which the rotifer feeds. Other rotifers are provided with various anterior grasping structures which enable them to capture larger prey, such as other rotifers. At the posterior end is the tail, which often bears a pair of toe-like processes, each containing a cement gland. The **anus,** reduced and non-functional in many species, is posterodorsal.

The **digestive system** includes a **pharynx** containing a grinding organ, the **mastax.** The components of this organ, the so-called **trophi,** are especially modified in relation to the food habits of the species, and their morphology has been found useful in taxonomy. The pharynx is also provided with a pair of **salivary glands.** Posterior to the pharynx are found, in order, an **esophagus,** a **stomach,** a short **intestine,** and a **cloaca.** The lining of the digestive tract is often a ciliated epithelium. Digestion appears to be mainly an extracellular process occurring under the influence of enzymes produced by glandular cells in the lining of the stomach. Epithelial cells in the stomach and intestine function also in the absorption and storage of the products of digestion.

Beneath the surface cuticle the body wall is composed of a simple ectodermal **epidermis;** the lining of the digestive tract is of endodermal origin. The tissues between these two layers are mesodermal, including muscle fibers and mesenchyme cells. An ill-defined body cavity is present but is not lined by a peritoneum. There is no circulatory system. A bilaterally arranged **protonephridial system** is present, opening anterolaterally at a pair of **nephridiopores.** The **nervous system** consists of a large ganglion lying dorsally in the head region and smaller ganglia in other parts of the body. Sense organs are generally distributed in the body wall. The system also includes nerve fibers interconnecting the ganglionic masses, sensory fibers from the receptors, and motor fibers innervating the muscle bands.

Rotifers are **dioecious;** that is, the sexes are separate. In one large group males are unknown, however, and reproduction occurs only by **parthenogenesis.** In other types sexual dimorphism is extreme, the males being much smaller and less well developed than the females. The **reproductive system** of the female includes compound organs, paired or single, which combine the

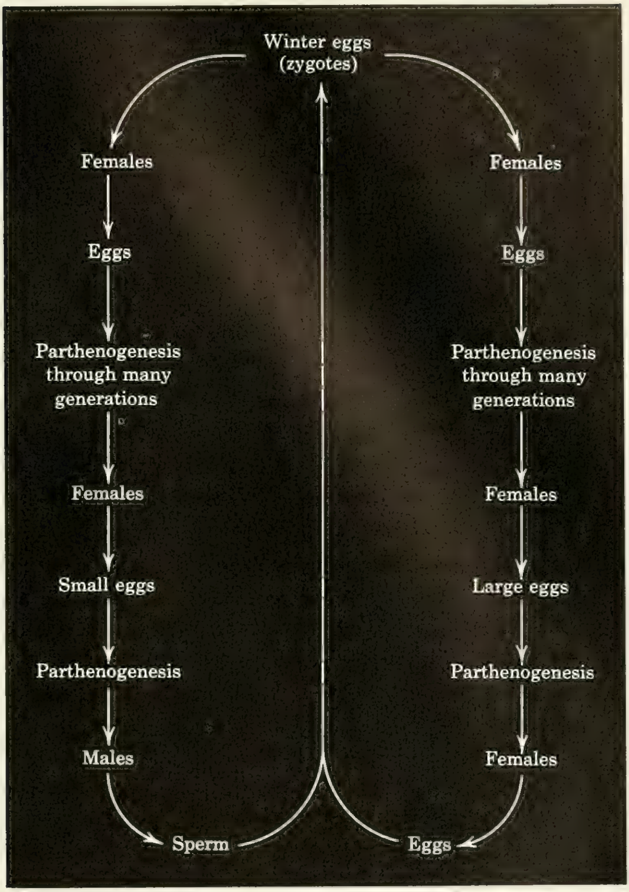

Winter eggs
(zygotes)
Females
Eggs
Parthenogenesis through many generations
Females
Small eggs
Parthenogenesis
Males
Sperm
Females
Eggs
Parthenogenesis through many generations
Females
Large eggs
Parthenogenesis
Females
Eggs

Fig. 12.2. Sequence of events in the life cycle of the rotifer, *Epiphanes senta.*

functions of **ovaries** and **yolk glands.** A short **oviduct,** continuous with the wall of this organ, leads posteriorly and opens into the cloaca. In the male there is usually a single, sac-like **testis;** spermatozoa reach the exterior through a simple **ductus deferens** which opens on the tail or posterior surface. A cuticular spine or **penis** may be developed. It appears that copulation does not usually occur; male gametes are injected into the pseudocoel of the female, and there is no regular site for insertion of the penis.

The **life histories** of rotifers have been the subject of much investigation. In some species, as mentioned previously, only females exist, and reproduction is exclusively parthenogenetic. In others numerous generations of females arise through parthenogenesis; eventually, as a result of some environmental change, eggs are produced that give rise, parthenogenetically, to either males or females. The eggs developed by these females require fertilization, and thus zygotes are formed. These zygotes, or "winter eggs," become surrounded by protective cysts and may remain dormant through long periods of unfavorable conditions. The life cycle recorded for *Epiphanes senta* (*Hydatina senta*), shown in Figure 12.2, indicates the complexity that is possible in rotifer life histories.

The tissues of rotifers are for the most part **syncytial**; that is, they consist of large masses of cytoplasm containing numerous nuclei but without distinguishable intervening cell membranes. An interesting peculiarity of rotifers, which they share with some other members of the phylum Aschelminthes, is that in each species the body contains a specific number of nuclei. Furthermore, each organ contains always the same number of nuclei. Normally, this constancy in nuclear number is established during embryonic development, and none of the nuclei is capable of subsequent division. A female, then, can deposit only as many eggs as there are germ cell nuclei in the ovary at the time of maturation; there is no continuous process of gametogenesis. The inability of the cells or nuclei of rotifers to divide also limits the regenerative powers of the animals. Under experimental conditions only very small parts can be successfully replaced by the animal—and only parts which do not contain nuclei.

Rotifers are important as animals with complex structure and life cycles, and as animals which constitute a significant group in the organization of a fresh-water environment. Classically, they have also been considered by phylogenesists as of possible significance from yet another standpoint. The rotifers exhibit a grade of organization roughly comparable to that of the so-called **trochophore larva**, characteristically found in the developmental cycles of many mollusks and annelids (pp. 375, 401). It should not be thought that rotifers are "persistent trochophores" in the strict sense; rotifers develop many extreme structural and functional specializations that are not characteristic of trochophore larvae. In general, however, the Rotifera may be thought of as representing a phylogenetic level of development which might well have produced also the trochophore-like ancestors of the mollusks and the segmented worms. This is an attractive theory, although the grounds upon which it rests are tenuous at best; if correct, it could do much to clarify the ancestral relationships between pseudocoelomate and eucoelomate animals.

The Class Nematoda. This class, from many standpoints the most important group of the aschelminths, is known principally through its parasitic members, which have long been familiar objects of study. Only comparatively recently has attention been directed toward the many species of free-living nematodes which occur in fantastic profusion in fresh water, salt water, moist soil, and other habitats. The populations of microscopic free-living nematodes inhabiting suitable environments are truly astronomical in numbers of individuals. Many species of nematodes are free-living at all stages in the life cycle, but perhaps the majority are parasitic at some time. It is possible to list a series of 19 general types of life cycles for the nematodes, ranging from the truly free-living forms with direct development, to a few wholly parasitic species. Many are free-living in younger stages and become parasitic in plants or in animals only as adults. Others may be parasitic as juveniles and leave the host at adulthood to become free-living. Therefore the line between "free-living" and "parasitic" species is difficult to draw, and it is virtually impossible to make a general statement describing the "typical" life cycle of the nematodes.

The body of a generalized nematode is a relatively simple, cylindrical tube, tapered at both ends (Fig. 12.3). Externally, the body is covered by a

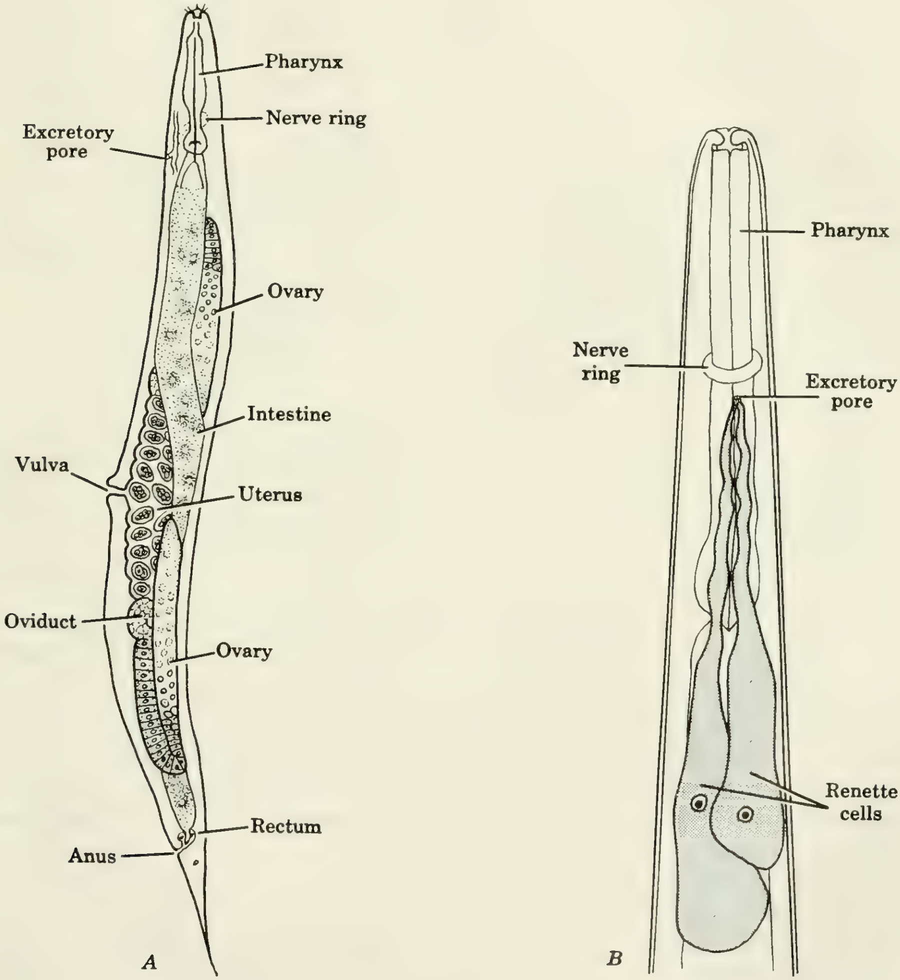

Pharynx
Nerve ring
Excretory pore
Ovary
Intestine
Vulva
Uterus
Oviduct
Ovary
Rectum
Anus
A
Pharynx
Nerve ring
Excretory pore
Renette cells
B

Fig. 12.3. Class Nematoda. *A*, a typical nematode, *Rhabditis maupasi*, adult female. In its juvenile stages this species is parasitic in the coelom and nephridia of earthworms. *B*, renette cells of a related nematode, *Rhabdias*. (*A*, redrawn, after G. E. Johnson, from C. G. Goodchild in F. A. Brown, Jr., *et al.*, *Selected Invertebrate Types*, copyright 1950 by John Wiley and Sons, Inc., printed by permission; *B*, redrawn, after B. G. Chitwood, from L. H. Hyman, *The Invertebrates: Acanthocephala, Aschelminthes, and Entoprocta*, copyright 1951 by McGraw-Hill Book Co., Inc., printed by permission.)

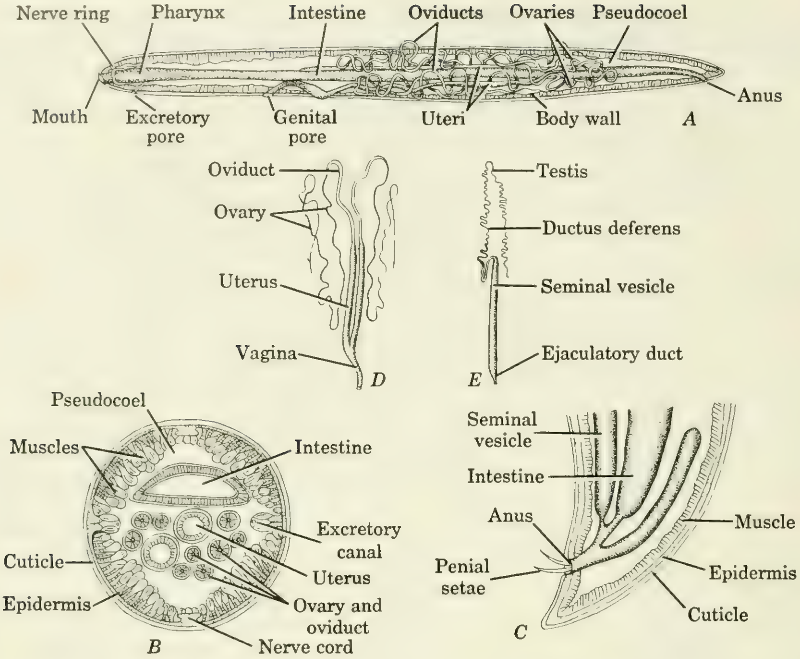

Nerve ring
Pharynx
Intestine
Oviducts
Ovaries
Pseudocoel
Anus
Mouth
Excretory pore
Genital pore
Uteri
Body wall
A
Oviduct
Ovary
Uterus
Vagina
D
Testis
Ductus deferens
Seminal vesicle
Ejaculatory duct
E
Pseudocoel
Muscles
Intestine
Excretory canal
Cuticle
Uterus
Epidermis
Ovary and oviduct
Nerve cord
B
Seminal vesicle
Intestine
Anus
Muscle
Penial setae
Epidermis
Cuticle
C

Fig. 12.4. *Ascaris lumbricoides:* general features of internal anatomy. *A*, dissection of a female, lateral view; diagrammatic. *B*, cross section in the midregion of the body. *C*, longitudinal section, posterior end of the male. *D*, female reproductive system. *E*, male reproductive system. (Modified after R. Leuckart, 1876, *Die menschlichen Parasiten.)*

cuticle, which must be molted periodically to permit growth of the individual. In free-living forms the cuticle often bears special structures, such as hooks, spines, and bristles; these usually function as locomotor appendages, as tactile organs, or as mouth parts to aid in feeding. Nematodes that are parasitic as adults are usually without such special structures, except for horny teeth and plates in the buccal cavity. In general, as among the Platyhelminthes, the parasitic forms appear to have undergone structural simplification in adaptation to their mode of life.

The simple **epidermis** of the body wall is underlain by a layer of peculiar **muscle cells,** usually organized in longitudinal bands. The typical muscle cell consists of a central cytoplasmic mass which contains a nucleus and gives rise to tremendously elongated contractile processes lying lengthwise underneath the epidermis. The muscular layer forms the external boundary of the pseudocoel, which contains a fluid presumably functioning in the transport of nutrients and wastes. The **digestive tract** is usually complete, consisting of a **mouth,** a muscular **pharynx,** an elongated **intestine,** a **rectum,** and a posterior **anus.** The intestinal epithelium, a single layer of tall, columnar cells bounded internally by a cuticular border, functions in whatever digestion may be necessary, as well as in the storage of reserves such as glycogen and lipids. Nematodes which are intestinal parasites, or which live amid decaying organic matter, either absorb or ingest food which has already undergone considerable decomposition; this obviates the need for elaborate digestive mechanisms.

The **nervous system** is centered in a circumpharyngeal **nerve ring,** from which nerve cords and fibers extend anteriorly and posteriorly. These fibers innervate the muscle cells and the sense organs. Although this is a relatively simple system, the coordination of activities which it brings about is remarkable.

Unlike most other Aschelminthes, the nematodes do not possess protonephridial systems. The function of **excretion** is served by a variously modified system of cells, sometimes with elongated intracellular canals, termed **renettes** (Fig. 12.3). These unique cells appear to function by absorbing wastes from the fluid in the pseudocoel and eliminating them at an excretory pore. There is no evidence in any known nematode for the existence of a protonephridial system; presumably this has been lost in the course of evolution.

The **reproductive mechanisms** of nematodes are relatively simple, although the life cycles are often complicated. The sexes are usually separate, and the gonads are tubular organs continuous with their paired, much elongated ducts. In the female the ducts join and open at a separate genital pore on the midventral line. In males the paired condition of the gonads is often lost; the paired or single sperm ducts proceed posteriorly and open into the rectum. Males are usually smaller than females and are provided with spines, called **penial setae,** which serve in copulation. In most marine and terrestrial nematodes there appears to be a tendency toward suppression of the male sex; many species show a large preponderance of female individuals. This is apparently not the case in fresh-water or parasitic forms.

Like the rotifers (p. 348), the nematodes are characterized by constant numbers of cells in their organs, or by constant numbers of nuclei in syncytial structures. Except in the germinal tissues, mitotic activity ceases at maturity, after a particular number of muscle cells, gut cells, etc., have been produced. In many of the larger parasitic nematodes there is a subsequent increase in the numbers of cells or nuclei as the worm grows, but this involves some kind of amitotic nuclear fragmentation.

Parasitic Nematoda: Ascaris lumbricoides. The adult worm, inhabiting the small intestine of man, is morphologically indistinguishable from the ascaris of swine and many other mammals. Larvae of the hog ascaris will not develop in man, however, and vice versa; therefore the hog ascaris is considered a separate subspecies or variety of *A. lumbricoides*. The female of this species (Fig. 12.4) is 8 to 16 inches in length, the male 6 to 8 inches. The overall characteristics of the species are similar to those described for a generalized nematode in the preceding section. In feeding, the intestinal contents of the host are drawn into the muscular pharynx of the worm and passed into its intestine. Here, absorption of this predigested mixture occurs;

as previously indicated, the intestinal epithelium of the nematode stores food reserves and transfers nutrients into the fluid of the pseudocoel, for distribution to all parts of the worm.

In *Ascaris*, **cellular metabolism** differs from the overall pattern found in most other animals because free oxygen is almost completely lacking in the intestine of the host. The release of energy in the cells of the ascaris occurs almost entirely by an anaerobic process, which in all its details is comparable to the anaerobic phase of cellular metabolism (pp. 36–37). Linked enzyme systems are present which in the absence of atmospheric oxygen are capable of partially oxidizing energy-rich carbohydrate molecules, such as glycogen, by decomposing them into various organic acids. This is a less efficient mode of energy release than the aerobic cycle; it has been imposed on the parasite by the conditions of its environment.

The reproductive organs of the ascaris are simple tubes, closed at their inner ends and lying free in the pseudocoel except for their attachments at the external openings. The posterior portions of the paired oviducts, in the female, expand to form the so-called **uteri**, which unite at the **vagina**. The male reproductive system in this species, as in many other nematodes, is unpaired (Fig. 12.4).

Spermatozoa, which in the ascaris are not flagellated but amoeboid, are introduced into the vagina at copulation. Ova are fertilized in the oviducts, and the resultant zygotes become surrounded by resistant proteinaceous shells secreted by oviducal glands. These eggs are released into the intestinal cavity of the host and reach the exterior with the host's feces. Development of the embryo to an infective juvenile stage occurs within the shell of the egg, at a rate which depends on external conditions. The young worms do not hatch until the eggs have been ingested by the proper host. When the juvenile thus reaches the intestine of man, it emerges, penetrates the intestinal mucosa, and reaches the circulatory system. It is carried by the blood through the liver and heart and to the lungs, where it enters an alveolus by rupturing a capillary. After molting and growing, the worm makes its way up the trachea and into the esophagus, eventually returning to the intestine as a small adult. Full growth and sexual maturity are finally attained after some time.

Infestation of man by *Ascaris lumbricoides* is not uncommon and is sometimes serious; the migrations of the juvenile worms through the body can give rise to widespread complications. Consideration of the mode of transfer from host to host shows clearly, however, that under modern conditions of sanitation infestation with *A. lumbricoides* is certainly avoidable.

Many other species of nematodes are dangerous parasites of man and domestic animals in different regions. For example, the **hookworms**, such as the American form, *Necator americanus*, and the related Old World hookworm, *Ancylostoma duodenale*, are intestinal parasites of man which in this country are more or less limited to warmer and more humid regions. Hookworms are armed with hook-like buccal plates with which they erode the intestinal lining

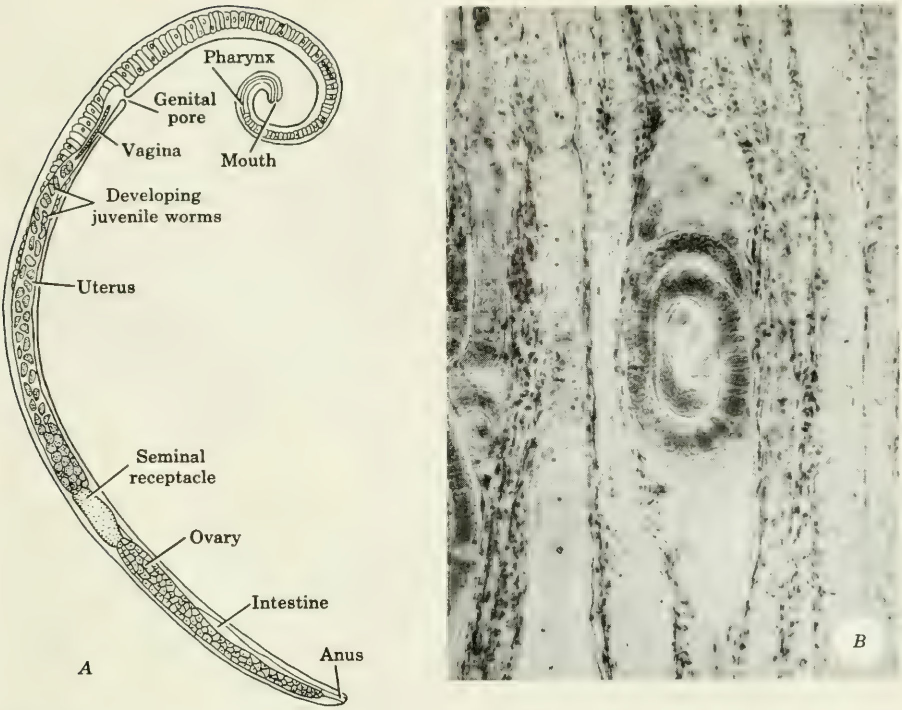


Fig. 12.5. Class Nematoda. *A*, adult female trichina worm, *Trichinella spiralis;* this stage inhabits the intestine of the host and produces thousands of juvenile worms which pass into the circulating blood and reach various tissues, chiefly muscles, where they encyst. *B*, encysted juvenile worm in striated muscle. (*A*, redrawn from C. G. Goodchild in F. A. Brown, Jr., *et al.*, *Selected Invertebrate Types*, copyright 1950 by John Wiley and Sons, Inc., printed by permission; *B*, photograph courtesy General Biological Supply House, Inc.)

of the host and ingest tissue fragments and blood. They are considerably more dangerous to the host than the ascaris, occurring in more massive infestations and causing serious loss of blood. Certain sections of the United States have undoubtedly been retarded in their development by the prevalence of hookworm infestations among the rural populations. As a result of active campaigns by public-health authorities and others, the situation has been much improved.

Other important nematode parasites of humans are the trichina worm, *Trichinella spiralis* (Fig. 12.5), which lives as an adult in the intestine of man and as encysted juveniles in the muscles of this host and a variety of others, including swine; and the filarial worms, such as *Wuchereria bancrofti*, which inhabits the lymph glands of man and requires a mosquito as an intermediate host. Details of the life cycles and pathological effects of these and many other interesting nematode parasites will be found in any textbook of parasitology.

THE ASCHELMINTH BODY PLAN

As stated at the outset, the phylum Aschelminthes is a very diverse group, and it is difficult to describe a body plan common to members of all the six classes. Certain characteristics are found in all the classes, however, and others occur in two or more. For instance, the nature of the body cavity is a major unifying feature. The condition of the body wall, with its cuticle, simple epidermal epithelium, and muscular layers bounding the pseudocoel externally, is also comparable throughout the phylum. A simple digestive system, marked in almost all groups by a well-developed, muscular pharynx, is common in aschelminths. The reproductive systems are variable, but we should consider the fact that many nematodes, for example, have undergone significant modifications in adaptation to the parasitic way of life.

OTHER PSEUDOCOELOMATE PHYLA

The Phylum Acanthocephala. Members of this phylum are usually cylindrical, worm-like animals; without exception, they are found in the adult stages as parasites of the digestive tracts of vertebrates. Their larvae occur in the bodies of invertebrate hosts, usually insects or crustaceans, which thus serve as intermediate hosts in the life cycles of the worms. Adult acanthocephalans of different species range in length from a small fraction of an inch to about 18 inches. Their most remarkable characteristics are the presence of a **proboscis**, armed with stout hooks, which has given them the name "thorny-headed worms," and the complete absence in all stages of any trace of a functional digestive tract. The proboscis, which is completely retractable into a sheath, serves to attach the parasite to the intestinal epithelium of the host. The damage inflicted on the gut lining of the host by the hooked proboscides of large numbers of these worms is chiefly responsible for the pathogenicity of the parasites.

The body of an acanthocephalan may be divided into an anterior **presoma**, bearing the proboscis, and a posterior **trunk** (Fig. 12.6). The body wall consists of a complex **cuticle** of several layers, permeated by a system of canals, and two well-developed **muscle layers**. The body cavity enclosed by the body wall is without a peritoneal lining and thus forms a pseudocoel. This space is occupied by a fluid and contains the excretory organs (compound protonephridia) and the reproductive system.

Acanthocephala are dioecious, and in common with most other parasitic worms they possess highly specialized and complex reproductive systems. Fertilization is internal, and development within the body of the female leads to the production of **acanthor larvae** (Fig. 12.7) enclosed in thick, resistant shells. These larvae are released by the parasite, reach the exterior with the feces of the host, and are ingested by the arthropod intermediate host. A period of further development within this host is required before the larvae become infective for the final host.

Fig. 12.6. A typical spiny-headed worm, *Acanthocephalus*. (Redrawn, after Yamaguti, from L. H. Hyman, *The Invertebrates: Acanthocephala, Aschelminthes, and Entoprocta*, copyright 1951 by McGraw-Hill Book Co., Inc., printed by permission.)

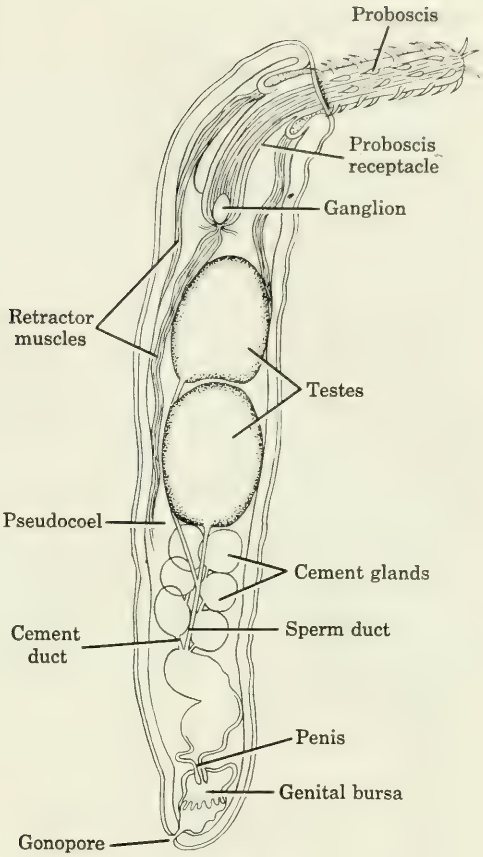
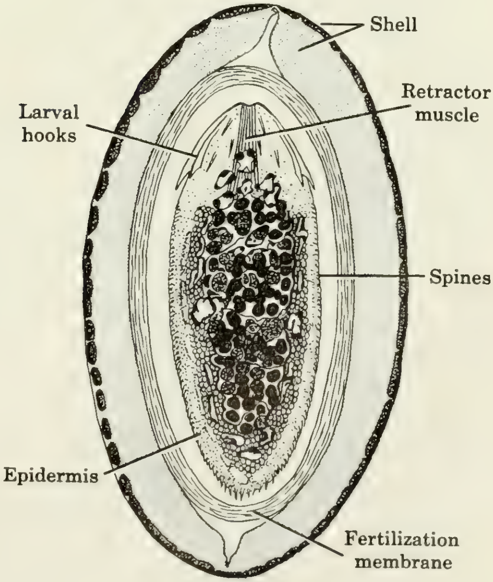

Proboscis
Proboscis receptacle
Ganglion
Retractor muscles
Testes
Pseudocoel
Cement glands
Sperm duct
Cement duct
Penis
Genital bursa
Gonopore

Fig. 12.7. Acanthor larva of the acanthocephalan *Macracanthorhynchus hirudinaceus*. This is the stage that enters the intermediate host, where it transforms into an **acanthella** larva. (Redrawn, after A. Meyer, from L. H. Hyman, *The Invertebrates: Acanthocephala, Aschelminthes, and Entoprocta*, copyright 1951 by McGraw-Hill Book Co., Inc., printed by permission.)


Shell
Retractor muscle
Larval hooks
Spines
Epidermis
Fertilization membrane

The tissues of acanthocephalans are largely syncytial, and as in rotifers and nematodes the number of nuclei represented in each organ of the body is relatively constant. Thus, for example, although a protonephridium may consist of hundreds of flame bulbs, the entire organ contains only three nuclei.

The taxonomic position of the acanthocephalans, and their possible affinities with other groups, are matters still subject to discussion. In many of their features they seem to show relationships to various members of the phylum Aschelminthes; in others they are somewhat similar to the class Cestoda of the phylum Platyhelminthes. Because they are pseudocoelomate, we have placed them near the aschelminths. It is clear that the Acanthocephala have behind them an extremely long history of endoparasitism, and that adaptations to this parasitic way of life have been so extensive as to mask their true relationships.

The Phylum Entoprocta. The members of this small phylum were originally confused with coelenterate polyps and later included with the Ectoprocta as a class of Bryozoa, or moss animalcules. They possess certain well-defined characteristics which make it logical to consider them as a separate phylum, allied to the aschelminths and acanthocephalans. The phylum contains a total of about 60 species; all are marine except members of the genus *Urnatella*, which inhabit fresh water. With some exceptions, entoprocts are colonial forms, the colony comprising a horizontally extended **stolon** from which the individual members arise at irregular intervals. Each individual consists of an upright **stalk** with a cup-shaped **calyx** at its tip; the organs are contained within the calyx. The upper rim of the calyx bears a ring of ciliated tentacles, which enclose a space termed the **vestibule.** At one side of this upper surface, within the circlet of tentacles, lies the **mouth;** the **anus** also lies within the vestibule, at the side opposite the mouth. The mouth and anus are connected by a U-shaped **digestive tract.** The organs of a typical entoproct are shown in Figure 12.8.

Surrounding the digestive tract is a pseudocoelic space largely filled with mesenchyme and containing the **reproductive organs,** a **central ganglion,** and a symmetrical pair of **protonephridia.** Reproduction involves fertilization of the eggs within the oviducts; the zygotes then emerge and attach to the floor of the vestibule, where early embryonic stages are passed. Eventually, free-swimming larvae are produced, which after a short period of free life attach to the substratum and undergo metamorphosis to adulthood. Colony formation follows the growth of a stolon from the base of the stalk of such a solitary individual.

Like rotifers, the ciliated larvae of entoprocts have been compared with the trochophores of mollusks and annelids (pp. 375, 401), although the similarities seem to be highly superficial and may be accounted for on the basis of convergent evolution in response to similar environmental conditions. Probably of greater significance is the marked resemblance between certain entoproct larvae and certain types of rotifers. Since the entoprocts are of the same grade of organization as the rotifers and are like them pseudocoelomate forms, they may well have evolved from an ancestral stock which also gave rise to the rotifers.

Minor Eucoelomate Phyla

THE PHYLUM ECTOPROCTA

Members of the phylum **Ectoprocta** are permanently attached, bilateral metazoans; most representatives develop extensive colonies, either arborescent or encrusting. In their possession of circumoral tentacles, they bear a superficial resemblance to coelenterate polyps and to entoprocts, and they have been classified with both of these groups. Increased knowledge of their structure has, however, revealed that the ectoprocts are of a higher grade of organization than either entoprocts or coelenterates.

Typically, each individual has a ciliated ridge surrounding the mouth and bearing many tentacles. This ridge, the **lophophore,** is circular in marine ectoprocts and horseshoe-shaped in the fresh-water types. This characteristic, among others, is a basis for the subdivision of the phylum into two classes. In all, the **anus** lies just outside the lophophore, and the digestive tract is consequently U-shaped. This arrangement is not uncommon in sessile metazoans.

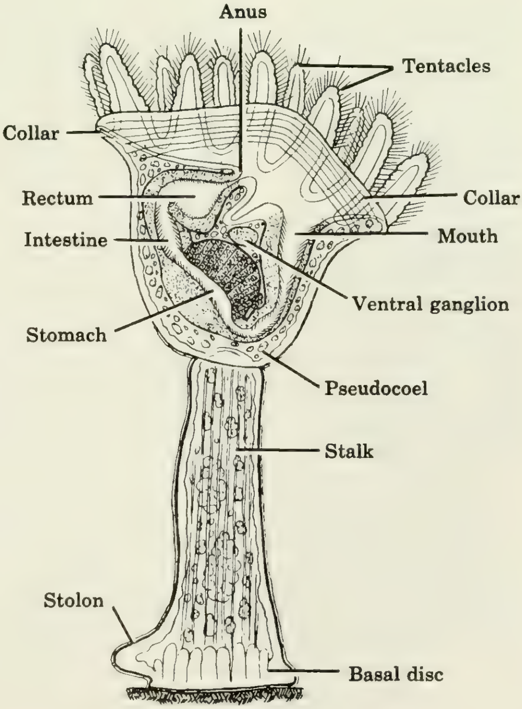


Fig. 12.8. An individual entoproct, *Pedicellina cernua.* This individual has developed by the metamorphosis of a larva. From the base of its stalk a stolon is beginning to form, which will grow horizontally over the substratum. From this stolon additional individuals will arise to form a colony. (From C. Cori in W. Kükenthal and T. Krumbach, 1933, *Handbuch der Zoologie.*)

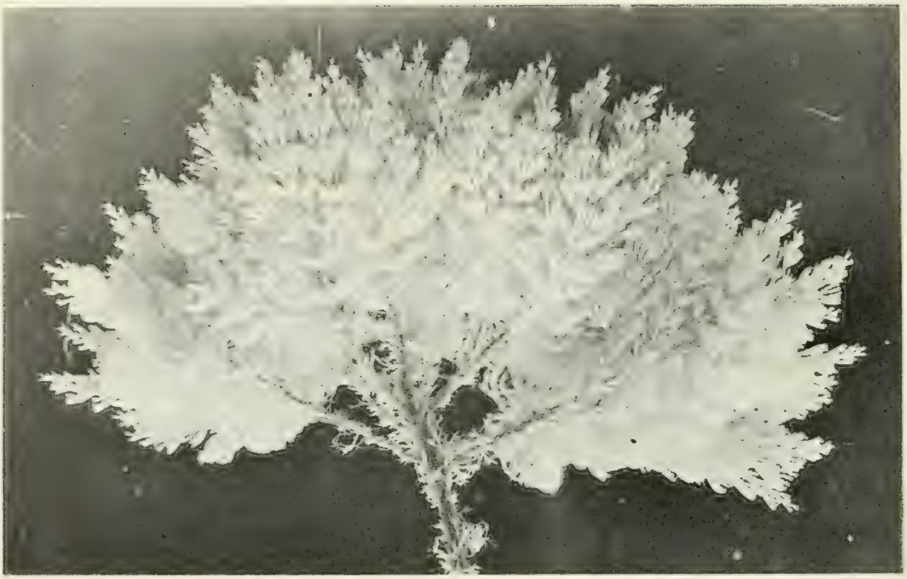


Fig. 12.9. The erect, branching colonial ectoproct, *Bugula*. (Photograph courtesy New York Zoological Society.)

The genus *Bugula*, members of which are abundant along our North Atlantic coast, is representative of the arborescent marine ectoprocts (Fig. 12.9). The individuals of the colony, termed **zooids,** grow in double rows on upright stalks branching from the original point of attachment of a single free-swimming larva. Each zooid is encased in a cuticular skeleton, into which the lophophore with its ring of ciliated tentacles may be completely withdrawn. The **anus** is located upon a collar-like region just below the lophophore and thus projects beyond the cuticular sheath when the lophophore is extended. Attached to the external surfaces of the major zooids are smaller, highly modified individuals termed **avicularia.** These resemble birds' heads; their large "beaks" are highly mobile and are opened and closed by powerful groups of muscles. By grasping and removing small objects with which they come in contact, the avicularia presumably function to keep the colony free of encrusting organisms.

Internally, the U-shaped **digestive tract** consists of a **pharynx,** a **stomach,** a **caecum,** an **intestine,** and a **rectum** (Fig. 12.10). *Bugula* is a ciliary particulate feeder, and its microscopic food is drawn into the mouth and driven into the pharynx by the action of the cilia. Here the food collects in masses which are moved through the digestive tract by the coordinated contractions of muscle fibers in the wall of the gut. Digestion occurs extracellularly, chiefly in the stomach, caecum, and intestine. Products of digestion are absorbed by the single-layered gastrodermal mucosa. Further transfer into the coelomic fluid probably occurs, and in the absence of a vascular system the coelomic fluid presumably serves as a circulatory medium. Excretory organs are lacking, although cells of the stomach epithelium appear to accumulate waste products in the form of brown granules. In older individuals these brown concretions are conspicuous, and eventually the entire body of the organism, with the exception of the cuticular sheath, progressively degenerates into a so-called "brown body." The significance of this process is not entirely clear.

The **nervous system** of the zooid is simple, consisting of a single ganglion in the region between mouth and anus, with fibers innervating sensory cells and muscle bands in the tentacles as well as other muscles in all parts of the body.

The coelom, probably developed by a schizocoelous process (p. 368), is lined by visceral and parietal peritoneum connected by a mesentery (**funiculus**)

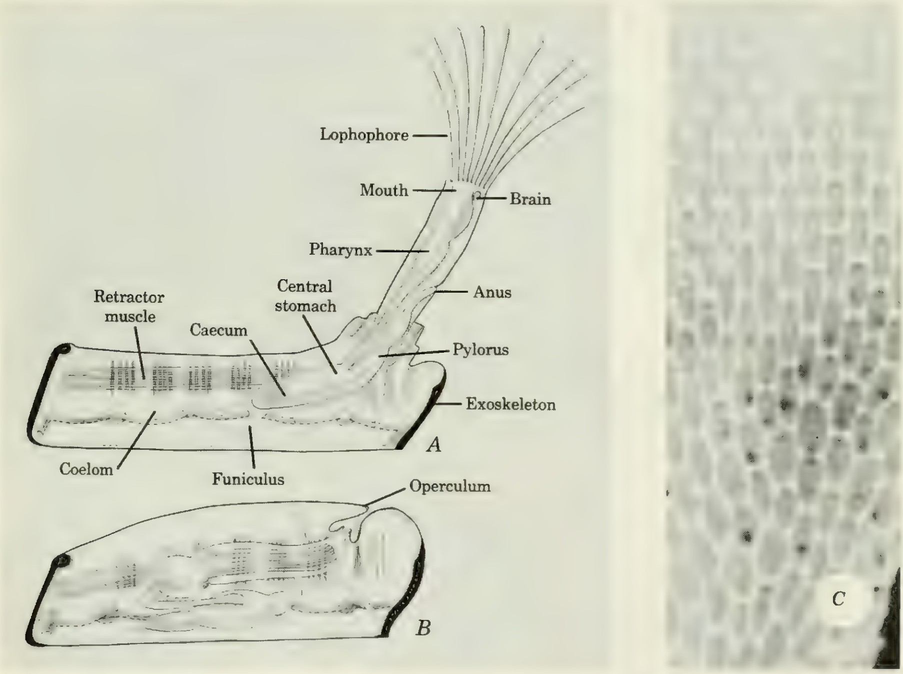


Fig. 12.10. General structure of an encrusting ectoproct, based on *Membranipora*. *A*, individual with lophophore extended; *B*, with lophophore retracted. In both diagrams the individual is represented as though sectioned along the midsagittal plane. The peritoneal lining of the coelom, and the remnants of mesenteries and septa, are indicated by broken lines. Note the position of the anus in relation to the circlet of tentacles about the mouth. *C*, surface view of a portion of a colony of *Membranipora tuberculata*, with all individuals retracted. Note the crescentic operculum at the anterior end of each individual. (*A* and *B*, redrawn from C. Cori in W. Kükenthal and T. Krumbach, 1938, *Handbuch der Zoologie; C*, photograph by George Lower.)

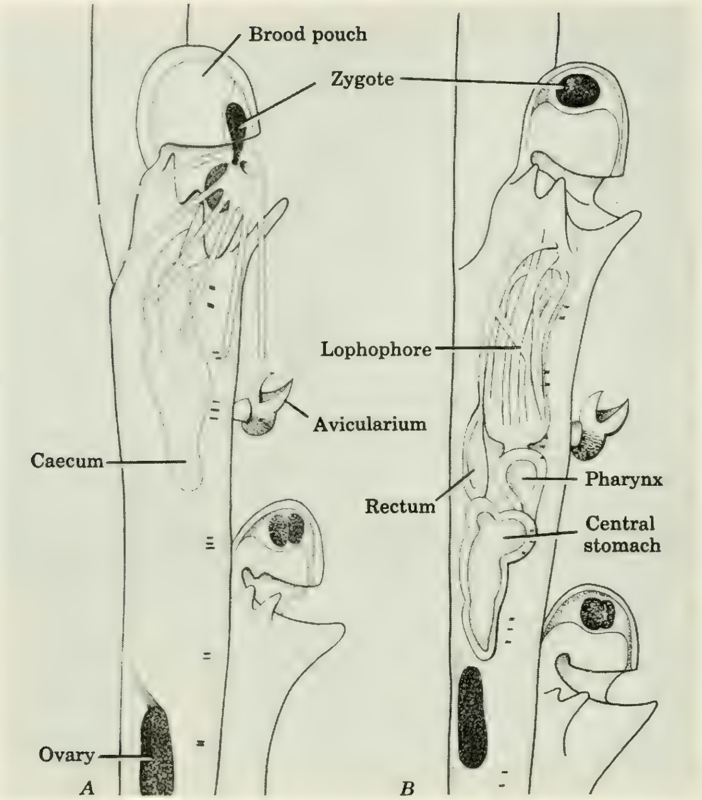


Fig. 12.11. *Bugula:* structure and reproduction. *A*, transfer of a zygote from the coelomic cavity of a zooid into the brood pouch, where it will develop into a ciliated larva. *B*, individual retracted and at rest; note the position of the lophophore within the vestibule. (Redrawn, after Gerwerghagen, from C. Cori in W. Kükenthal and T. Krumbach, 1938, *Handbuch der Zoologie.*)

extending from the end of the caecum to the posterior body wall. This mesentery usually bears the **testis**, and an **ovary** develops in the parietal peritoneum of the same individual. Fertilization of a single ovum occurs within the coelom, and the zygote is passed forward into a **brood pouch** which develops like a hood extending distally over the lophophore (Fig. 12.11). Within this pouch the embryo matures, becoming a ciliated larva which escapes for a brief period of free existence. With the release of this larva, a second egg matures in the ovary, is fertilized, and takes its place in the brood pouch. The free-swimming larva (Fig. 12.12) settles upon the substratum, and its ensuing development into a mature animal involves a radical metamorphosis. In this transformation practically all signs of organization are lost, the organs of the future adult arising from an apparently undifferentiated mass of cells. The individual thus developed soon produces other zooids by a process of budding, and a branching colony is formed. The majority of the marine relatives of *Bugula* have similar life cycles but form plate-like, encrusting colonies in which each zooid is encased in a rigid, limy shell or zooecium (Fig. 12.10).

The colonies of ectoprocts in fresh water are also of two types. Some are branching, like *Plumatella*, which is supported by a skeleton of chitinous material. In others, such as *Pectinatella*, the skeletal secretion takes the form of a large, gelatinous mass, in the surface layers of which the bodies of the zooids are embedded (Fig. 12.13). These fresh-water ectoprocts reproduce sexually and also by an asexual process involving the formation of internal buds, or **statoblasts**. These become covered by hard, brown, chitinous shells and in autumn and winter may be found in large numbers floating or entangled in submerged vegetation. Like the gemmules of sponges (pp. 280–281), they can withstand freezing, desiccation, and other unfavorable conditions and eventually germinate to develop into new colonies.

THE PHYLUM BRACHIOPODA

The Brachiopoda, or lamp shells, are marine animals attached to the substratum by a stalk and enclosed in bivalve shells somewhat resembling those of clams. In the brachiopods, however, the valves appear to be paired dorso-

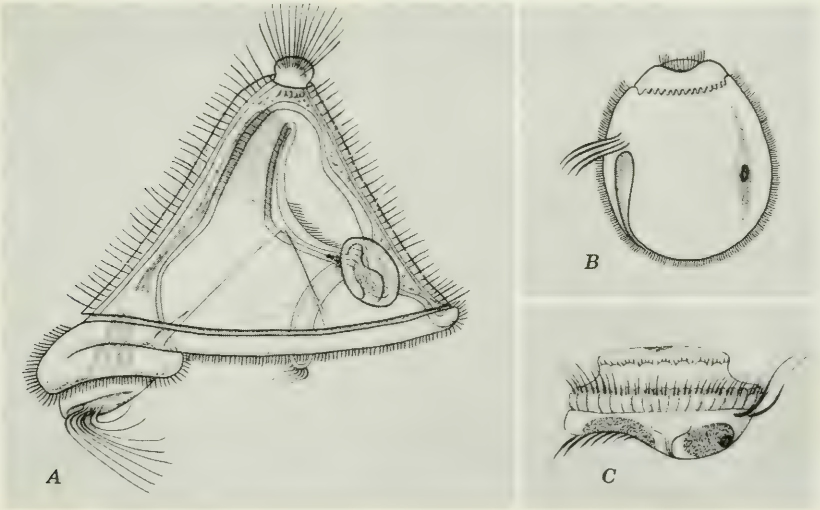


Fig. 12.12. Larvae of marine ectoprocts. *A*, cyphonautes larva of *Electra pilosa;* this is a feeding stage, with a complete digestive tract. *B*, non-feeding, transitory larva of *Bugula*. *C*, larva of *Alcyonidium;* note the reduced and non-functional digestive cavity. (Redrawn, after various authors, from C. Cori in W. Kükenthal and T. Krumbach, 1938, *Handbuch der Zoologie*.)

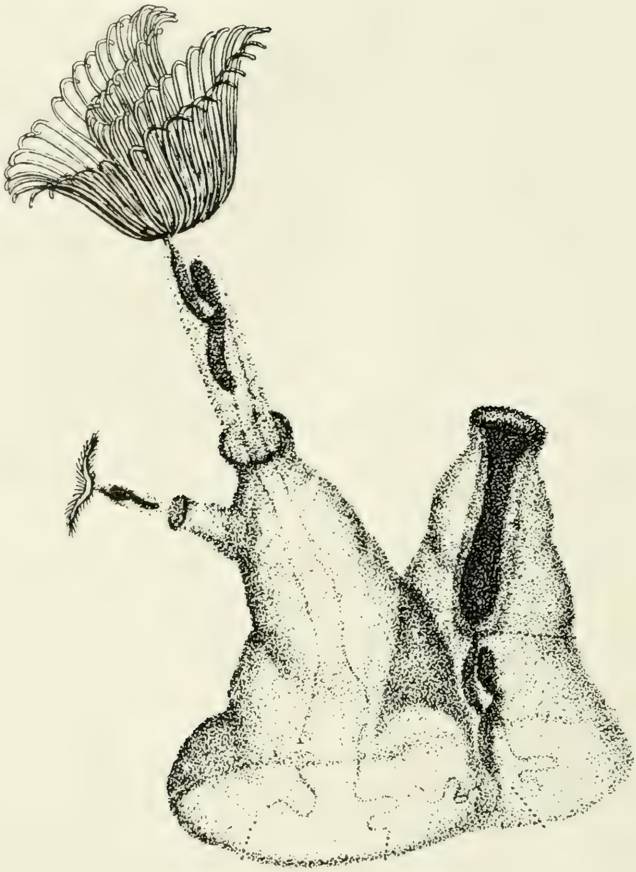


Fig. 12.13. Portion of a colony of the fresh-water ectoproct *Lophopus crystallinus*. Note the horseshoe-shaped lophophore of the expanded individual, the U-shaped digestive tract, and the opening of the anus outside the ciliated tentacle crown. The individual at the right is retracted; at the left is a recently formed bud. (Reproduced from the engraving by Lyonet in Abraham Trembley, *Histoire de Polypes*, Leyden, 1744. This work contains the original description of the species and is accurate in all details. For other contributions of Trembley, see Figure 10.5.)

ventrally, and in clams they are lateral. Furthermore, the enclosed body of the brachiopod bears no resemblance to that of a mollusk.

Brachiopods are usually divided into two classes. In the more primitive of these, represented by species of the genus *Lingula* (Fig. 12.14), the valves of the shell are delicate and chitinous and are not directly hinged upon one another. There is a long, fleshy stalk, occupied by an extension of the coelom; an anus is present; and the lophophore is without any calcareous support. Members of the other class, represented by *Terebratulina* (Fig. 12.14). possess heavier, limy shells which are hinged together; the stalk is generally short, solid, and fibrous; no anus is present; and a calcareous "shelly loop" supports the lophophore. Fundamental differences also appear in the embryonic development of the two groups.

The brachiopods are an ancient group. Not more than 260 species are now known to be living; but more than 7000 species have been recorded as fossils. The existing genus *Lingula* is represented by species in the earliest fossil-bearing rocks of the Cambrian period (roughly half a billion years old) and in later deposits. Our present species have apparently undergone very little modification, and this is probably the oldest known genus of animals represented among our contemporary fauna.

The genus *Terebratulina* represents the great majority of modern brachiopods. The calcareous valves of the shell are both opened and closed by specific groups of muscles, and other groups of muscles adjust the position of the animal in relation to its stalk. The upper (dorsal?) valve is the smaller

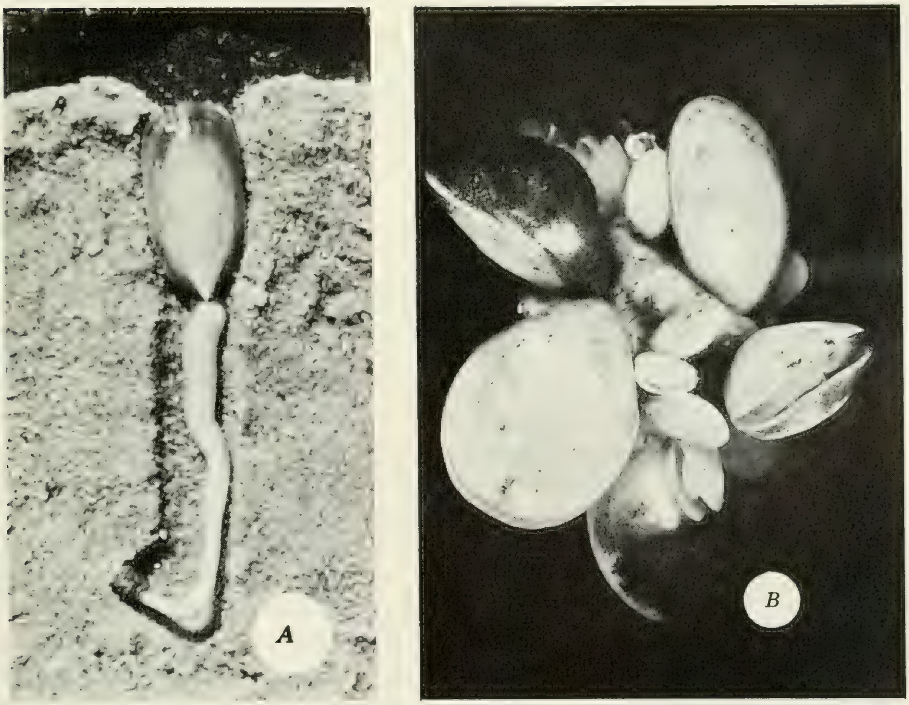


Fig. 12.14. Representative Brachiopoda. *A*, *Lingula*, shown in its burrow in a sandy sea bottom; *Lingula* is a modern example of a type of organization that has persisted with little change through about half a billion years of the earth's history. *B*, *Terebratulina*, representing a more progressive type which has developed heavier calcareous valves, hinged together, and a calcareous support for the lophophore. This tentacle-bearing feeding structure can be seen in the individual with partly opened valves. (*A*, photograph by Eugene S. Clark, Jr.; *B*, photograph by George Lower.)

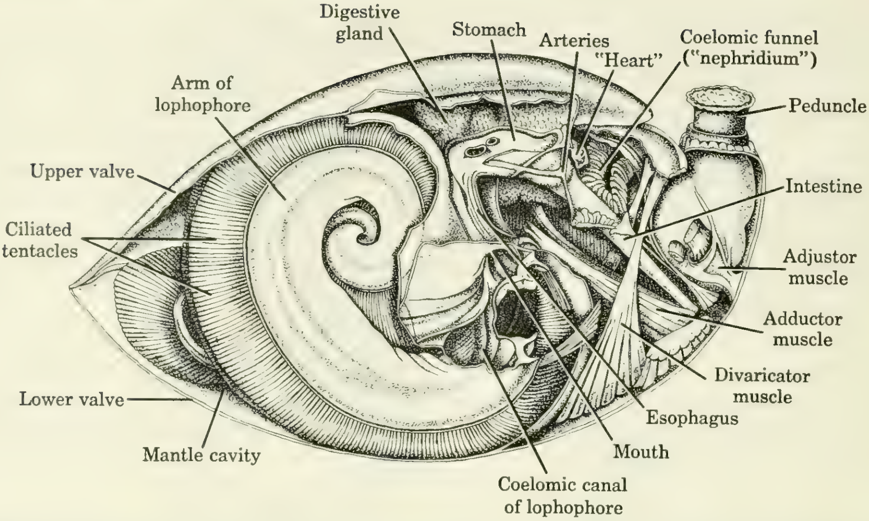

Digestive gland
Stomach
Arteries
"Heart"
Coelomic funnel ("nephridium")
Arm of lophophore
Peduncle
Upper valve
Intestine
Ciliated tentacles
Adjustor muscle
Adductor muscle
Divaricator muscle
Lower valve
Esophagus
Mantle cavity
Mouth
Coelomic canal of lophophore

Fig. 12.15. Lateral view of a brachiopod, *Magellania flavescens*, partially dissected from the left side to show general arrangement of internal organs. The left arm of the lophophore has been removed, along with other structures. *Magellania* is generally similar to *Terebratulina* (*cf.* Fig. 12.14). (Redrawn from A. Hancock, 1858, *Philosophical Transactions of the Royal Society of London*, vol. 148.)

and fits like a lid upon the lower (Fig. 12.15). The short stalk extends upward through the posterior margin of the lower valve, then curves abruptly downward to the substrate. Internally, the most conspicuous feature is the horseshoe-shaped **lophophore**, which bears ciliated tentacles and occupies a large part of the cavity between the valves. The arms of the lophophore converge upon the **mouth**, and ciliated grooves in these arms conduct microscopic food particles into the mouth opening. The mouth leads into a simple digestive cavity consisting of **gullet**, **stomach**, and **intestine**. Both stomach and intestine are provided with branching digestive glands. As previously indicated, an **anus** is lacking in *Terebratulina* and its relatives. A **circulatory system** is present, with extensive ramifications throughout the body and into the tentacles. Coelomic sinuses, lined by a ciliated peritoneum, also permeate the body, and the function of circulation is probably shared to some extent between the coelomic fluid and the blood. The **nervous system** is simple, consisting of a nerve ring surrounding the gullet and giving off numerous branches. The **gonads** are branched organs occupying coelomic sinuses in the mantle flaps lining the valves. Sexes are separate. Eggs or sperms are discharged into the coelom and make their way to the outside through a pair of ciliated funnels often termed **nephridia**. Whether these organs actually function as nephridia, or whether their chief function is that of gonoducts, is open to question. Fertilization is external, although development into a ciliated, free-swimming larva may occur within the mantle cavity of the female in a sort of brood chamber. After a brief period of free existence, the larva settles upon the substrate, develops a stalk for attachment, and undergoes a metamorphosis into the adult condition.

THE PHYLUM CHAETOGNATHA

The phylum **Chaetognatha** consists of small marine animals, called "arrow worms." Their precise relationship to other phyla is doubtful, but their

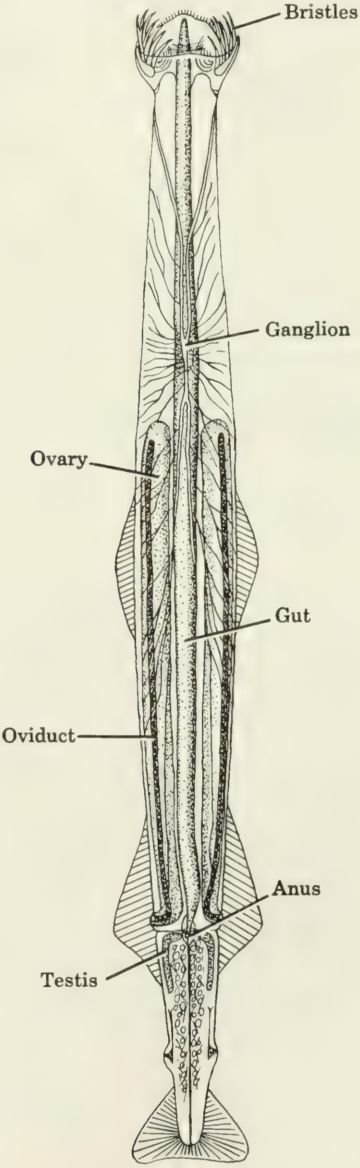


Fig. 12.16. Anatomy of a typical chaetognath, *Sagitta hexaptera*, ventral aspect. (Redrawn, after O. Hertwig, from C. Schneider, 1902, *Lehrbuch der vergleichenden Histologie der Tiere*.)

enterocoelous development indicates a position somewhere near the evolutionary stem which culminated in the Chordata. Members of the genus *Sagitta* (Fig. 12.16) are pelagic forms, often very abundant in the marine plankton, swimming by means of body movements and horizontal fins. There are prehensile mouth parts consisting of a series of stout, chitinous hooks, suggesting the name Chaetognatha, or "bristle jaws." A relatively large coelom is divided transversely into three compartments by septa, and there are also dorsal and ventral mesenteries linking the gut wall and the body wall. The **nervous system** consists of a dorsal ganglion, from which nerve cords extend as a circumpharyngeal ring to a ventral ganglion, with nerve fibers radiating to all parts of the body. The animals are monoecious, and the zygotes develop into miniature adults without a ciliated larval stage.

Summary

In this chapter we have discussed several groups of metazoan animals which have little in common except their triploblastic, bilateral organization. Each of these groups, with the exception of the Aschelminthes, presents a consistent pattern of general characteristics sufficiently different from those of all other animals to warrant their status as separate phyla. There remains some doubt among zoologists about the validity of erecting a phylum Aschelminthes to contain the widely different forms proposed for inclusion, of which we have discussed only two; the pseudocoelous body cavity is their chief unifying characteristic.

The members of each of the phyla considered in this chapter have undergone extensive modification in their evolution, in adaptation to particular ways of life or conditions in their environments. As evidence of their evolutionary histories and phylogenetic affinities there remain only the most general and fundamental characteristics. These enable us to determine the approximate level of organization which each type represents but not to state with any confidence the true relationships of any of these groups. We may conclude that although they are interesting from the biological standpoint, perhaps none of them has been of great significance in relation to the evolution of the major phyla of animals.

In the chapters to follow we shall discuss the major invertebrate groups—phyla which have been successful, as judged from the numbers of species and of individual organisms they contain. Generally speaking, these major groups retain sufficiently significant characteristics to permit us to establish, with some probability, their phylogenetic relationships.

CHAPTER 13

CHAPTER 13

THE PHYLUM MOLLUSCA

Schizocoela and Enterocoela

The major groups of eucoelomate animals constitute two great divergent stocks, distinguishable on the basis of several fundamental differences. These differences involve such features as the type of cleavage, the time in development when the cellular precursors of the various organs become differentiated, and the relationship of the blastopore to the axial polarity of the embryo and the future adult. In addition, there are basic differences in the mode of formation of the mesoderm and of the coelom, and it is from this particular characteristic that the terms **Schizocoela** and **Enterocoela** are derived. In the schizocoelous forms, comprising the major phyla Mollusca, Annelida, and Arthropoda and several minor phyla, the mesoderm of the adult arises by proliferation of cells called **mesoblasts,** set aside early in the cleavage process. The coelom forms as a result of the development of cavities within the solid masses of mesodermal cells so produced. In the enterocoelous forms, on the other hand, represented by the major phyla Echinodermata, Hemichordata, and Chordata, the mesoderm appears primitively as hollow outgrowths from the wall of the embryonic gastrocoel, and the coelomic cavities develop as enlargements of the spaces within these evaginations.

It should be understood that from the point of divergence of these two stocks the phylogenetic tree of animals consists of two major branches, in each of which evolution has proceeded independently of the other (see Fig. 7.3, p. 219). The schizocoelous branch culminates in the great phylum Arthropoda, and the enterocoelous branch has reached its apex in the phylum

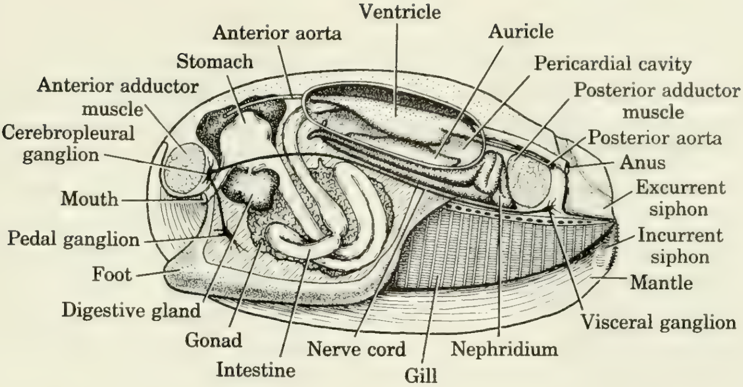

Ventricle
Anterior aorta
Auricle
Stomach
Pericardial cavity
Anterior adductor muscle
Posterior adductor muscle
Cerebropleural ganglion
Posterior aorta
Anus
Mouth
Excurrent siphon
Pedal ganglion
Incurrent siphon
Foot
Mantle
Digestive gland
Visceral ganglion
Gonad
Nerve cord
Nephridium
Intestine
Gill

Fig. 13.1. Internal structure of a typical fresh-water pelecypod, drawn as though the left valve had been removed and the body dissected from the left side; semidiagrammatic.

Chordata. From the standpoint of numbers of species and individuals, as well as of adaptability to various environmental situations, each of these climax groups represents a markedly successful type of organization. It is fruitless to speculate about which is "higher," an arthropod or a chordate, or about which of these evolutionary lines has produced the more successful type of animal.

In this and subsequent chapters, we shall consider first the schizocoelous phyla, beginning with the phylum Mollusca, and then the enterocoelous animals.

The Phylum Mollusca

The Mollusca may be defined as bilateral, unsegmented, triploblastic animals, typically with a calcareous exoskeleton. The body is divided into **head, foot,** and **visceral** regions, and a single pair of compound excretory organs is present. Except in certain specialized members of the phylum, the body is enclosed by a characteristic outgrowth of the body wall, the **mantle,** which is responsible for the secretion of the exoskeleton. The word Mollusca is derived from the Latin *molluscum*, meaning soft, and refers to the texture of the body within the shell. The phylum consists of five classes: the class **Amphineura,** or chitons, typically flattened forms with segmented dorsal shell plates; the class **Gastropoda,** represented by the snails and slugs; the class **Pelecypoda,** or bivalve mollusks such as clams and mussels; the class **Scapho-**

poda, a small group of unfamiliar marine animals called "tooth shells"; and the class **Cephalopoda**, the squids, cuttlefishes, and nautili.

The majority of mollusks are free-living animals, adapted to a creeping or burrowing existence and provided with a protective shell into which the extensible soft parts can be withdrawn. Such mollusks as the cephalopods, however, are modified for a more active, free-swimming habit. Most mollusks are marine animals and are abundant in shallow waters but not at great depths. The sea seems to have been the primitive habitat, but many species of gastropods and pelecypods are found in fresh water, and gastropods are common also on land. The more representative types were classified as Mollusca by Aristotle, Linnaeus, and Cuvier, but in the early classifications this group included many animals which have since been distributed among other phyla. Many different kinds of mollusks are used as food today, and archaeological evidence indicates that shellfish were a very important item in the diet of many primitive humans.

In this chapter we shall examine particularly the characteristics of bivalve mollusks such as the clam and the fresh-water mussel, as animals typical of this grade of organization, to be compared with the hydra, the planarian, the earthworm, and the vertebrate.

THE CLASS PELECYPODA

The Clam or Fresh-Water Mussel: ***General Structure and Activities.*** The following account is applicable to any of the common marine clams, such as *Venus mercenaria*, or to the fresh-water mussels such as species of the genera *Lampsilis* or *Anodonta*. The shell is composed of two **valves**, fitted together at the dorsal side to form a **hinge** which is covered externally by a tough, elastic **hinge ligament**. The dome-like part of each valve, lying near the hinge, is termed the **umbo** (plural, **umbones**); this is the oldest part of the shell, as indicated by the **rings of growth** which surround the umbo and mark the successive outlines of the growing shell. The valves are **lateral**; the hinge ligament is **dorsal**; the gape of the valves is **ventral**. The umbones generally lie just **anterior** to the midline of the shell, although between different species of bivalves this characteristic is subject to much variation. Looking at a clam with its valves intact reveals nothing of the living animal itself, except as the **foot** may be thrust out between the margins of the shell, or the tube-like **siphons** extended posteriorly.

Removing the shell reveals the external surface of the clam. Closely appressed to the internal surface of each valve is a flap of the **mantle** (Fig. 13.1). On each side, the mantle represents a sheet-like outgrowth of the dorsolateral body wall. Its functions include the secretion of the shell, the various layers of which are produced by specialized tracts of glandular cells at the edges of the mantle and on its external surface. Passing through the mantle on both sides are the fibrous masses of the **anterior** and **posterior adductor muscles**; these course directly from one valve to the other and are attached to the valves at roughened areas termed **muscle scars.** Contraction of the powerful adductor muscles brings about closure of the valves. When the muscles relax, the elasticity of the hinge ligament causes the valves to gape ventrally. Other muscle masses, **retractors** and **protractors,** are variously developed in different species. Generally speaking, they occur in pairs both anteriorly and posteriorly, originating in the body wall of the clam and inserting near the adductor muscles on the internal surfaces of the valves. In effect, the retractor muscles suspend the body of the organism from the valves, and variation of their states of contraction and relaxation adjusts the position of the animal within the shell. Enclosed between the two flaps of the mantle is a space, the **mantle cavity,** filled with circulating water. The ventral edges of the mantle flaps, held closely together at the margins of the valves, effectively seal off the mantle cavity from the external environment. The posterior margins of the mantle, however, are modified into two extensible tubes, the **siphons,** through which the mantle cavity communicates with the surrounding water. The siphons may be protruded between the valves, and in *Venus mercenaria* they are provided with special triangular **siphon retractor muscles** attached to each valve. Through the **ventral** or **incurrent siphon** water is drawn into the mantle cavity; through the **dorsal** or **excurrent siphon** it is conducted outward.

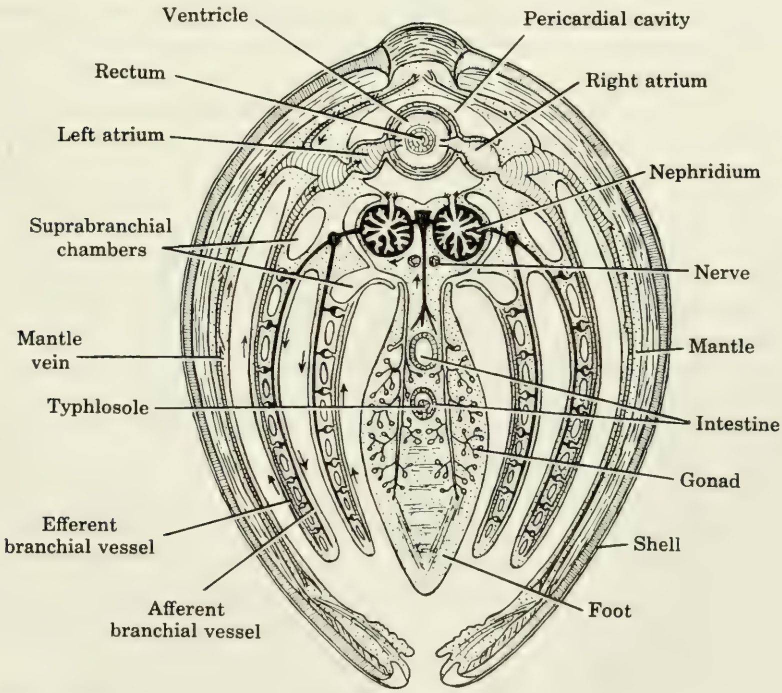

Ventricle
Pericardial cavity
Rectum
Right atrium
Left atrium
Nephridium
Suprabranchial chambers
Nerve
Mantle vein
Mantle
Typhlosole
Intestine
Gonad
Efferent branchial vessel
Shell
Afferent branchial vessel
Foot

Fig. 13.2. Diagrammatic cross section of a typical fresh-water pelecypod, *Anodonta*, showing the heart and principal blood vessels. (From W. Stempell, 1926, *Zoologie im Grundriss.*)

The major portion of the body, the **visceral mass**, occupies the central part of the mantle cavity. The **foot** is an extensive, flexible, muscular region attached along the ventral margin of the visceral mass and continuous with it. On each side of the body a pair of plate-like **gills**, each composed of rows of parallel **water tubes**, hangs down into the mantle cavity between the visceral mass and the mantle (Figs. 13.1, 13.2). Anterior to the gills are the **labial palps**, which, like the gills, are paired. The **mouth** lies in the angle between the anterior end of the foot and the anterior adductor muscle, and the palps are connected across the midline by ridges which extend transversely and form lip-like structures above and below the mouth.

In its normal position, embedded in the sandy or muddy bottom of a body of water, the animal usually lies with the median plane vertical and only the posterodorsal margins of the valves visible. Ordinarily, the valves are held slightly agape, and the siphons protrude into the water. The action of cilia on surfaces bounding the mantle cavity maintains a gentle circulation of water, passing in through the ventral siphon, circulating in the mantle cavity and through the gills, and finally moving outward through the dorsal siphon. In locomotion the foot is thrust forward and either expanded at its tip or turned so that it takes a clumsy hold in the sand or mud of the bottom. The body is then drawn forward by the contraction of the powerful muscles of the foot.

Structures and Functions Related to Metabolism and Responsiveness. During the following discussion, it should be borne in mind that the entire "economy" of the clam is based on the circulation of water through the mantle cavity. Powerful cilia on the mantle, on the surfaces of the visceral mass, on the gills, and on the palps function to maintain this circulation. The organism depends on these currents of water for food, for the elimination of egesta and excreta, for exchange of respiratory gases, and very often for the dispersal of gametes and zygotes.

The water entering the mantle cavity through the incurrent siphon is drawn through the **ostia**, minute openings on the surfaces of the gills, into the **water tubes**, and through these vertical passages upward to the **suprabranchial chambers**. There are four of these chambers, one lying above each gill and parallel to the longitudinal axis of the body. The suprabranchial chambers unite beneath the posterior adductor muscle to form a region known as the **excurrent chamber**, or **cloaca**, which opens externally by way of the excurrent siphon. In the course of this circulation through the gills, **gaseous exchange** is effected between the water and the circulating blood. Microscopic particles of food borne by the water entering the mantle cavity are sifted out by the cilia on the gills, or are entangled in sheets of mucus secreted by the mantle and the surface of the visceral mass. These food particles and food-laden sheets of mucus are moved toward the palps by specifically oriented ciliary pathways, and finally are conducted into the mouth by cilia on the palps. The palps appear to exercise a certain amount of selectivity, largely on the basis of weight: heavier particles are dropped by the palps and gather ventrally in the mantle cavity. Here they are bound together by mucus and eliminated through the incurrent siphon by periodic vigorous contractions of the adductor muscles. Among the mollusks the ciliary-mucus feeding mechanism is best developed in the pelecypods, although some sessile gastropods have evolved a similar method. Certain tube-dwelling annelids and a few primitive chordates also depend on ciliary currents and sheets of mucus to entrap their microscopic food.

The **digestive system** of the clam consists of **mouth, esophagus, stomach, intestine, rectum,** and **anus** (Fig. 13.1). The esophagus is short and leads directly into the stomach, which also receives the openings of a pair of branching **digestive diverticula.** The stomach of many pelecypods is provided with another diverticulum, the **style sac,** which secretes and holds in its lumen a semisolid, gelatinous rod, the **crystalline style.** This rod is kept in constant rotation by the cilia lining the sac, and its free end protrudes into the cavity of the stomach, where its substance gradually and continuously dissolves. This rod is essentially a mass of the secretion products of gland cells in the style sac. It contains digestive enzymes, largely **amylases,** which are released into the stomach to function in the preliminary steps of the digestive process. Particles of partially digested food are conducted by ciliary currents into the branching lumen of the digestive diverticula, where digestion is continued. Finally, particles of food are engulfed by cells lining the passages within the diverticula, and the process of digestion is completed intracellularly. **Absorption** occurs in the diverticula, and to some extent in the anterior parts of the intestine. The major function of the relatively long intestine and rectum appears to involve the dehydration and concentration of digestive wastes into fecal pellets or strands, which are eliminated at the anus into the outflowing streams of water in the cloaca.

The well-developed **circulatory system** constitutes what might be called an "open" system. A pulsatile **heart** is present, consisting of a pair of lateral **atria** (auricles) and a thick-walled, tubular **ventricle** (Fig. 13.2). The ventricle is wrapped around the rectum, but this fact appears to have no functional significance. From the ventricle spring an **anterior** and a **posterior aorta.** These are the chief distributing vessels which carry blood through specific branches to the various organs of the body, including the foot, the mantle, the gills, the excretory organs, the alimentary canal, and so on. Within these organs the blood flows through spaces which are not lined by a continuous endothelium, and thus are **sinuses** rather than **capillaries.** In such an "open" system the nutrients and oxygen carried in the blood may diffuse directly into the intercellular fluid, without passing through the walls of blood vessels. This would appear advantageous; but, in comparison with capillary systems, the efficiency of a system of sinuses is reduced by the fact that blood pressure is necessarily low, and the velocity of flow is likewise diminished. After its circuit through the tissues, the blood is returned by collecting vessels into the thin-walled atria and thence into the ventricle. The course of this circulation is diagrammatically presented in Figure 13.3.

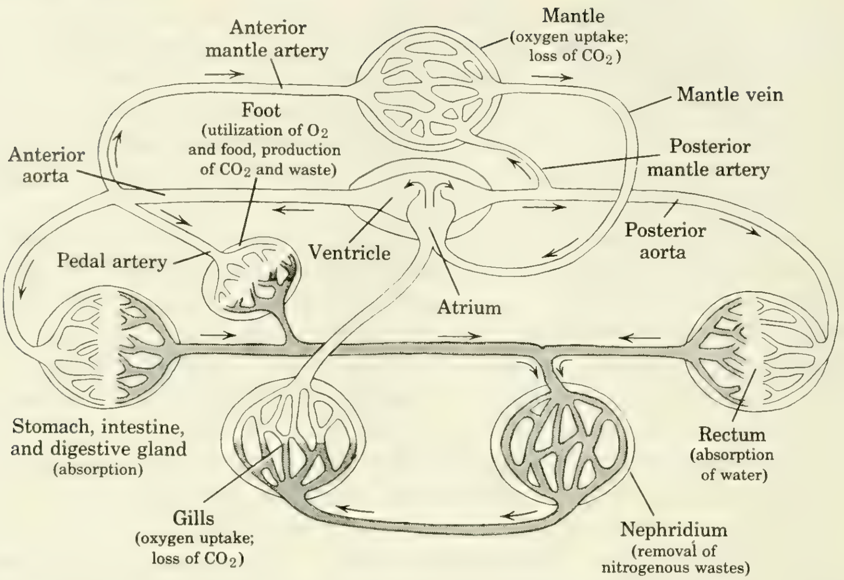

Anterior mantle artery
Mantle (oxygen uptake; loss of CO_2)
Mantle vein
Foot (utilization of O_2 and food, production of CO_2 and waste)
Anterior aorta
Posterior mantle artery
Posterior aorta
Pedal artery
Ventricle
Atrium
Stomach, intestine, and digestive gland (absorption)
Rectum (absorption of water)
Gills (oxygen uptake; loss of CO_2)
Nephridium (removal of nitrogenous wastes)

Fig. 13.3. Schematic diagram of the course of circulation in a pelecypod. In bilaterally paired organs, only one member of the pair is shown. Arterial vessels are clear, venous channels stippled.

Mollusks are clearly coelomate animals, but in the adult pelecypod the coelom is very much reduced. It is represented chiefly by the cavity in which the heart lies, the so-called **pericardial cavity.** This chamber is also related to the **excretory organs,** which are paired tubes or **nephridia** leading from the anterior end of the coelom to external openings in the suprabranchial chambers of the inner gills. Each nephridium is folded upon itself and is differentiated into glandular and bladder-like portions. The structure and relationships are such that excreta in solution within the coelomic, or pericardial, cavity may enter the tubule; or excreta carried by the circulating blood may be extracted by the cells in the glandular portion of the nephridium. The details of the process of excretion are not fully known.

The **nervous system** consists of a pair of **cerebropleural ganglia,** one on each side of the mouth; a pair of **pedal ganglia** in the foot; and a pair of **visceral ganglia** lying on the ventral surface of the posterior adductor muscle. Commissures unite the ganglia of each pair, and **cerebropedal** and **cerebrovisceral connectives** course between the brain and the other chief ganglion pairs. Nerves extend from the ganglia to the sensory surfaces of the body and to the muscles. The chief sense organs in clams and mussels include **tactile organs,** such as the papillae of the siphons, which are also sensitive to light; the **osphradia,** two areas of sensory epithelium near the visceral ganglia which function as chemoreceptors; and a pair of **statocysts,** organs sensitive to changes in position, located in the foot near the pedal ganglia. Among the pelecypods, *Pecten*, the scallop (Fig. 13.4), is noteworthy for its possession of numerous well-developed **eyes** along the margins of the mantle. These eyes are not capable of image formation but are differentially sensitive to gradual and to rapid changes in illumination.

Activities related to **metabolism** and **responsiveness** in clams and mussels resemble, so far as they are known, those of other animals of a comparable level of complexity. Most pelecypods are sluggish animals, with a comparatively low rate of metabolism, relatively inactive habits, and a simple sensory-neuro-muscular system.

Reproductive Organs, Reproduction, and Development. In most clams and fresh-water mussels the sexes are separate, although in successive breeding seasons the same individual may function first as a male, then as a female. The **ovaries** and **testes** are extensively branching structures embedded in the visceral mass, among the coils of the intestine. Their ducts open into the suprabranchial chambers near the nephridiopores. The reproductive processes in the marine clams, which will be described first, are vastly different from those of many fresh-water mussels. In *Venus mercenaria*, the common marine hard-shell clam or "quahaug," the gametes are shed into the open water of the sea, reaching the exterior through the excurrent siphon. Fertilization occurs externally, and the zygotes develop into free-swimming, ciliated **trochophore larvae**. These soon transform into a second larval stage, the **veliger**, which develops the precursors of the mantle and begins to secrete the shell. Veligers by gradual changes become young clams, which at first are fastened to the substratum by a thread, the **byssus**. They

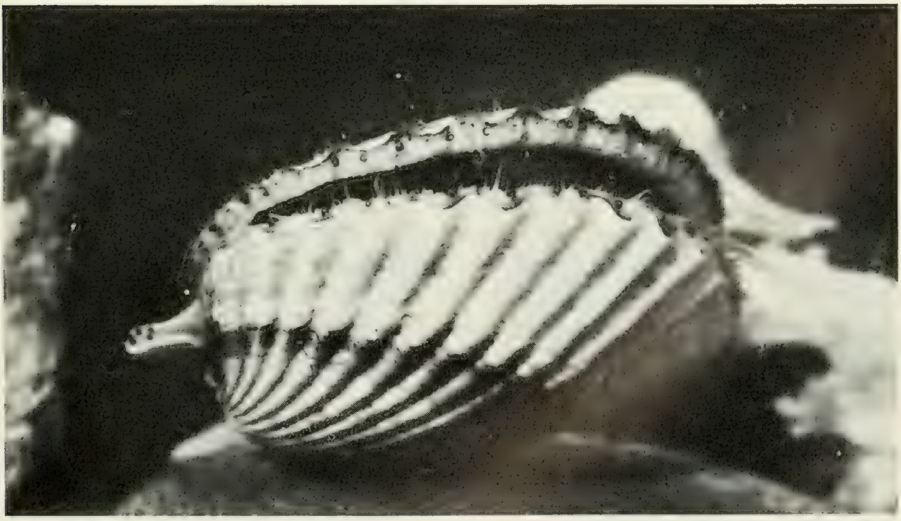


Fig. 13.4. A scallop, *Pecten irradians*, showing sensory tentacles and eyes at the edge of the mantle. (Photograph by Eugene S. Clark, Jr.)

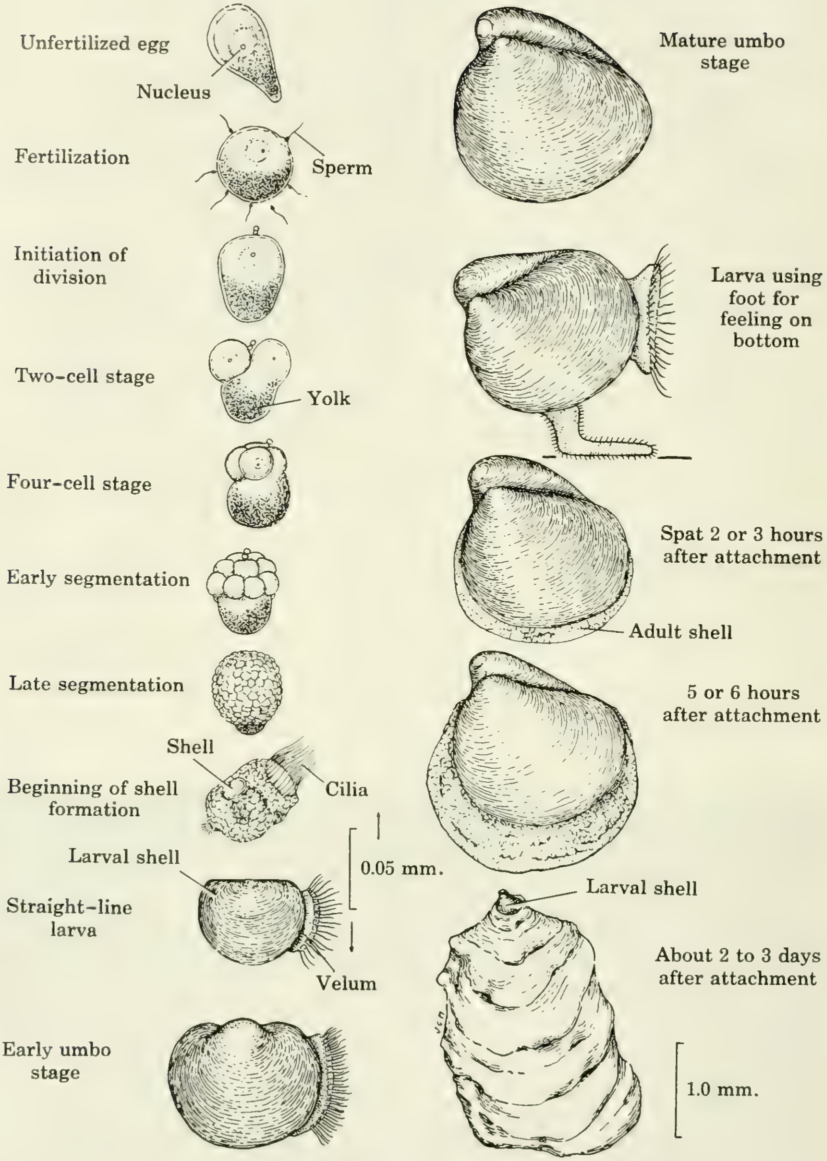

Unfertilized egg
Nucleus
Fertilization
Sperm
Initiation of division
Two-cell stage
Yolk
Four-cell stage
Early segmentation
Late segmentation
Shell
Beginning of shell formation
Cilia
Larval shell
Straight-line larva
0.05 mm.
Velum
Early umbo stage
Mature umbo stage
Larva using foot for feeling on bottom
Spat 2 or 3 hours after attachment
Adult shell
5 or 6 hours after attachment
Larval shell
About 2 to 3 days after attachment
1.0 mm.

Fig. 13.5. Developmental stages of the oyster, *Crassostrea virginica*. Note the progressive loss of bilateral symmetry just before and after attachment of the young oyster. The stage marked "Beginning of shell formation" corresponds essentially to the trochophore stage; the "Straight-line larva" is a veliger. (From C. L. Newcombe and R. W. Menzel, 1945, Contribution No. 22, Virginia Fisheries Laboratory.)

eventually become free, burrow in the bottom, and develop to maturity within a few years (cf. Fig. 13.5).

The majority of the larger fresh-water mussels, such as *Lampsilis*, *Anodonta*, *Quadrula*, and others, exhibit a very interesting life cycle which involves a larval stage parasitic on fresh-water fishes. In these mussels the spermatozoa released by the male are drawn into the mantle cavity of the female. After passing through the gills, they encounter ova which have been discharged into the suprabranchial chamber, and fertilization occurs. The zygotes are transferred into specialized parts of the gills of the female, varying in different species, which serve as **brood chambers**, and the early developmental stages are passed within these pouches. The result of these changes is a larval stage called the **glochidium**, a microscopic form possessing a bivalve shell, with hooks and well-developed adductor muscles, and often a long, thread-like byssus (Fig. 13.6). These larvae are emitted from the body of the female and lie on the bottom, with their valves gaping and the byssus extending upward in the water. Contact with the proper species of fish stimulates the contraction of the adductor muscles, and the valves of the shell clamp shut upon fin rays, gill filaments, or other exposed parts of the fish. The young parasite is subsequently overgrown by tissues of the host and remains in this situation for a variable period of time, eventually leaving the host to begin its free life upon the bottom. Like the majority of parasitic animals, glochidia are specialists in the sense that they can live and develop in only one or a few related species of hosts. The glochidia of most species parasitize fishes; one species, however, is known to develop on the mud-puppy, *Necturus*.

Life cycles involving parasitic larval stages are not the invariable rule among fresh-water mussels. In some species, as in members of the genus *Sphaerium*, the eggs are fertilized and develop into miniature adults within brood pouches formed in the gills of the female.

Other Functions: Shell Formation. One of the chief functions of the mantle in bivalve mollusks concerns the secretion of the calcareous shell. The shell itself consists of three layers differing in composition and appearance. Externally, the valve is covered by a thin, proteinaceous **periostracum**, often tan, greenish, brown, or black in color. Beneath the periostracum lies the **prismatic layer**, composed of spicules of calcium carbonate laid down within an organic matrix. The prismatic layer is chiefly responsible for the bulk and strength of the shell. The valve is lined internally by a so-called **nacreous layer**, generally smooth and highly polished and often showing the beautiful, iridescent coloring characteristic of "mother of pearl." The nacreous layer contains a higher proportion of organic material than the prismatic layer. The margins of the mantle appear to be most active in the secretion of the shell. The periostracum is laid down by special cells in this region, and in normal growth the calcareous layers are added to the margins of the valve by this part of the mantle. Recent investigations have shown that the edge of the mantle and adjacent regions are more active in the deposition of calcium salts than other parts. Damage to the shell, how-

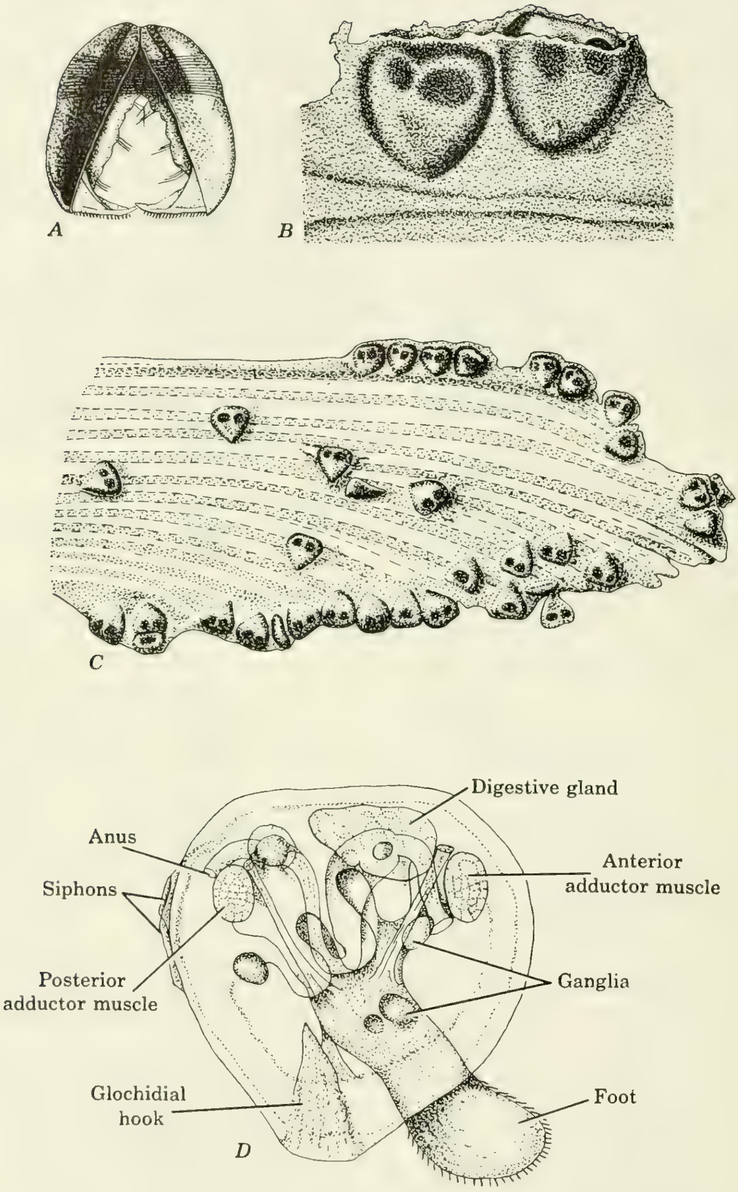

A
B
C
Digestive gland
Anus
Anterior adductor muscle
Siphons
Ganglia
Posterior adductor muscle
Glochidial hook
Foot
D

Fig. 13.6. Developmental stages of fresh-water mussels. *A*, hooked glochidium of *Symphynota* before attachment to fish. *B*, young glochidia of *Anodonta* 24 hours after attachment to the fin of a carp. *C*, glochidia of *Anodonta*, 36 hours after attachment, well embedded in the tissue of the fin. *D*, juvenile mussel, *Symphynota*, after termination of the parasitic phase; note adult structures already formed and persistence of the glochidial hook. (Redrawn from G. Lefevre and W. C. Curtis, 1910, *Bulletin of the U.S. Bureau of Fisheries*, vol. 30.)

ever, even in regions near the umbo, is successfully repaired by the secretory activities of the underlying mantle surface.

Pearls. The formation of a pearl by a bivalve is an abnormal manifestation of its shell-forming activities. Any small foreign body, such as a sand grain or a parasite, coming to lie between the mantle and the valve, is enfolded by the mantle in a small invaginated pocket. Copious secretion of **nacre** by the epithelium of the pocket follows, and the foreign particle becomes coated with successive layers of this material. Many years may be required for the growth of a large pearl. In Japan, a flourishing industry has grown from the discovery that a small piece of shell inserted into a pocket of the mantle in the pearl oyster, *Pinctada*, will in the course of several years be transformed into a commercially valuable "cultured" pearl. Oysters bearing such implanted seeds are maintained in wire cages and carefully tended to insure a maximal rate of growth. Pearls are found occasionally in fresh-water mussels, but they are generally irregular in shape and of inferior color.

Other Pelecypoda. Although the bivalved shell can be recognized without difficulty in almost all species, there is great diversity in the superficial appearance of pelecypods. Interesting differences are shown, for example, with respect to the relative sizes and positions of anterior and posterior adductor muscles. In such forms as *Venus mercenaria* and the fresh-water mussels, the two adductors are about equally developed; this is considered the primitive condition. In another group, exemplified by the marine mussel, *Mytilus*, the anterior adductor is much smaller than the posterior, and a line drawn between the two muscles would lie at an angle to the hinge axis. In such forms as the oyster, *Crassostrea*, and the scallop, *Pecten*, the anterior adductor is lacking, and only the posterior adductor remains to close the valves (Figs. 13.4, 13.7).

Other variable characteristics include the size and weight of the shell and the size and development of the foot and siphons. In sedentary species such as the oyster, the foot is very much reduced, and in such burrowing forms as *Ensis*, the razor clam, and *Mya*, the "steamer," the foot is very large (Fig. 13.8). Adaptation to the habit of burrowing deeply into mud or peat, into rock, and into wooden structures exposed to salt water commonly involves reduction and modification of the shell and increase in the size and length of

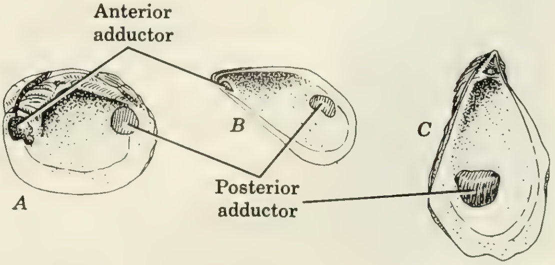


Fig. 13.7. Shells of bivalve mollusks, showing attachments and relative sizes of anterior and posterior adductor muscles. *A*, a fresh-water mussel; *B*, marine mussel, *Mytilus; C*, oyster, *Crassostrea*, which in the adult stage lacks an anterior adductor muscle.

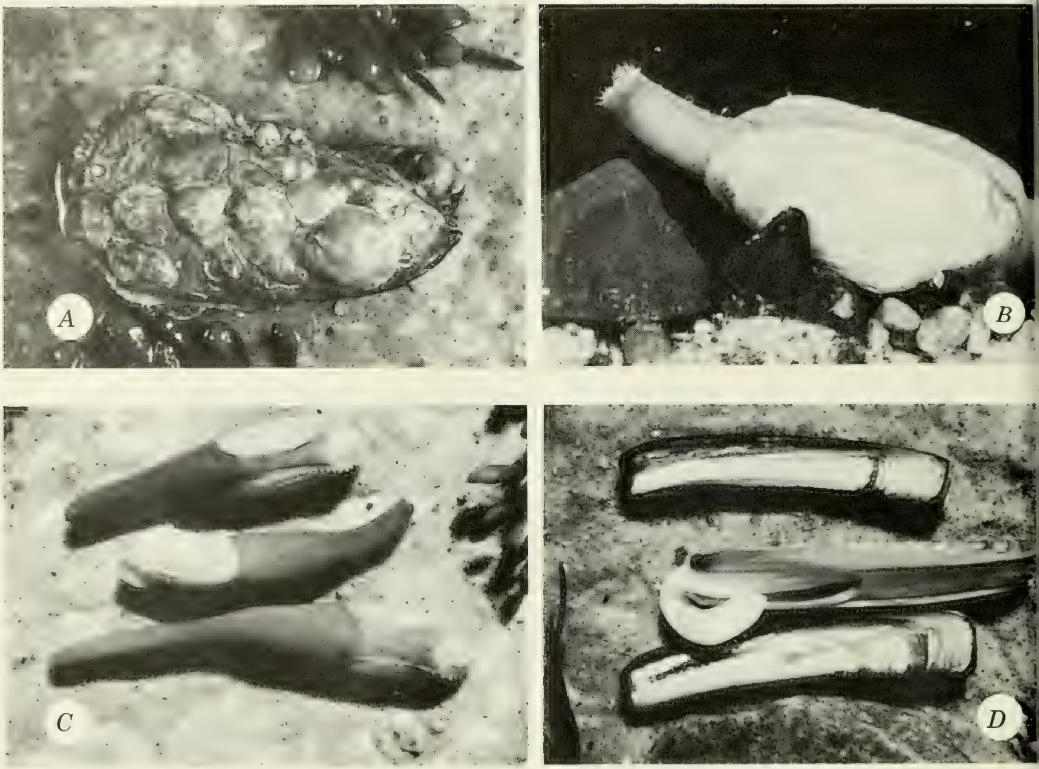


Fig. 13.8. Variously modified bivalves. *A*, two sedentary species: an oyster, *Crassostrea*, encrusted with jingles, *Anomia simplex*. *B*, *C*, and *D*, burrowing and boring forms: *B*, *Mya arenaria; C, Barnea truncata; D, Ensis directus.* Forms like *Mya* and *Ensis*, burrowing in soft sand and mud, possess enlarged and elongated siphons and somewhat reduced shells, with well-developed feet. *Barnea*, which bores into harder mud or peat, has a much reduced foot, highly specialized shells, and elongate siphons. (*A*, *C*, and *D*, photographs by Eugene S. Clark, Jr.; *B*, photograph by Charles Walcott.)

the foot and the siphons. The anterior ends of the valves often develop special cutting edges, as in *Barnea* (Fig. 13.8). Perhaps the most highly specialized and aberrant of the boring bivalves is the shipworm type, represented by *Teredo* and related forms. This animal derives its common name from its extremely elongate, worm-like appearance, and from the fact that it burrows into the planking of wooden boats or any other submerged wood not artificially protected. The siphons, which protrude from the burrow posteriorly, and the greatly reduced bivalve shell, which constitutes the anterior boring mechanism, are marks of the pelecypod nature of this bizarre clam (Fig. 13.9).

For comparison with other mollusks, the members of the class Pelecypoda are characterized by lateral compression, by the bivalve shell, and by modification of the entire organization in relation to a mode of feeding which is unusual among the other classes.

THE CLASS AMPHINEURA

The amphineurans are well exemplified by the chitons, or "armadillo snails." These mollusks are frequently encountered at the seashore, although in numbers of species and in abundance they are insignificant when compared with pelecypods or gastropods. The shell consists of eight dorsal plates, in

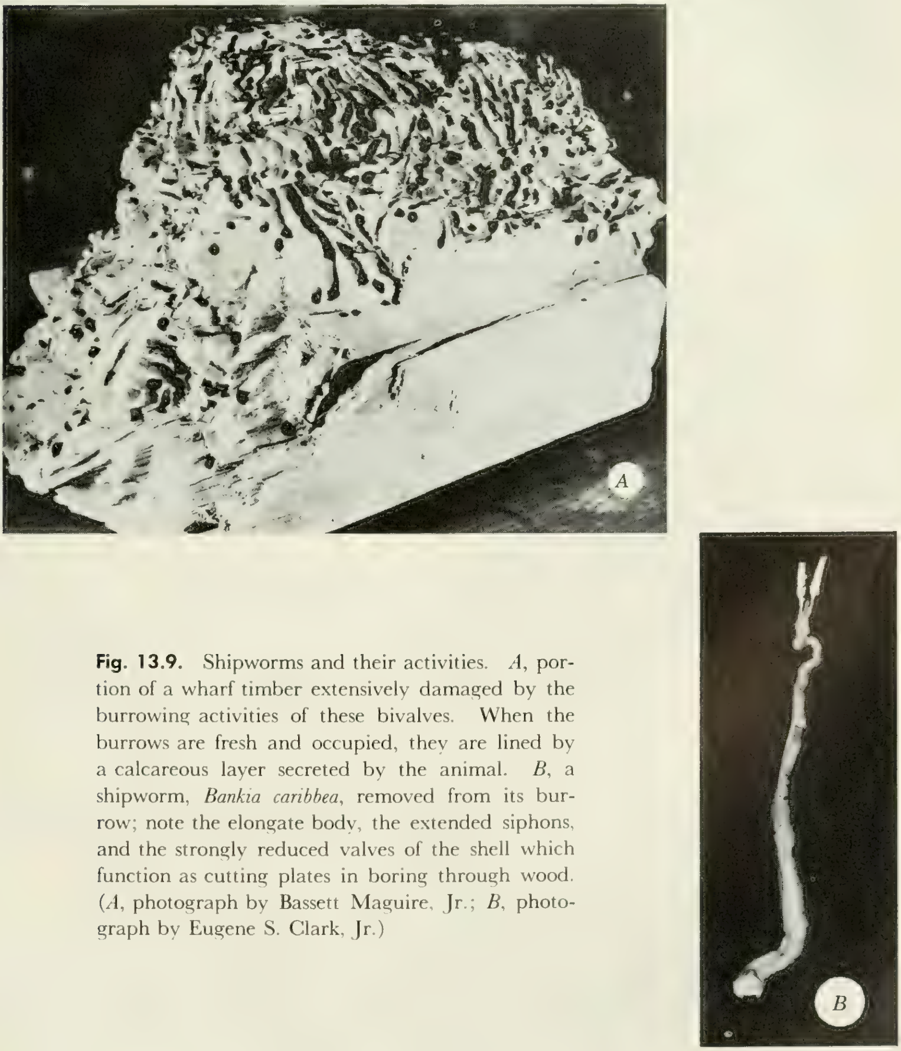


Fig. 13.9. Shipworms and their activities. *A*, portion of a wharf timber extensively damaged by the burrowing activities of these bivalves. When the burrows are fresh and occupied, they are lined by a calcareous layer secreted by the animal. *B*, a shipworm, *Bankia caribbea*, removed from its burrow; note the elongate body, the extended siphons, and the strongly reduced valves of the shell which function as cutting plates in boring through wood. (*A*, photograph by Bassett Maguire, Jr.; *B*, photograph by Eugene S. Clark, Jr.)

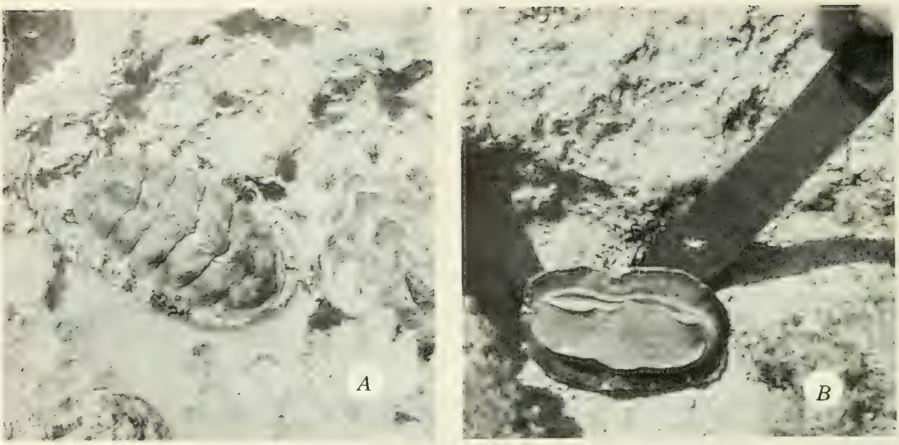


Fig. 13.10. A chiton, dorsal and ventral views. The segmented skeletal plates are bounded laterally by a peripheral fold of the mantle. In *B*, the broad foot has been released from its attachment to the substratum; note the lateral row of gills, protected by the overhanging mantle fold. (Photographs by John F. Storr.)

some species concealed by an overlying integument. The ventral **foot** is broad and flat, modified for creeping and for adhesion to stones and other smooth surfaces (Fig. 13.10). The edge of the body, forming the **mantle,** surrounds the foot dorsolaterally. In the angle between foot and mantle a row of small **gills** extends into the mantle cavity on each side. An anterior region, covered dorsally by the overhanging mantle and distinct from the foot, constitutes the **head** and bears the **mouth.** The **anus** opens posteriorly into the mantle cavity, between the paired **nephridiopores** and **reproductive openings.**

Chitons live in shallow water in rocky localities, creeping slowly or lying with the edges of the body firmly fixed against the substratum. Their food consists of algae which are rasped from the rocks by the action of a tongue-like **radula** resembling that of a snail (p. 384). Internally, the digestive, circulatory, excretory, reproductive, and nervous systems are generally similar to those described for pelecypods, but less well developed and of a relatively primitive type.

Amphineurans are believed to resemble more closely than any other existing type of mollusk the common ancestral form from which all have evolved.

THE CLASS GASTROPODA

The gastropods, represented by the snails and slugs, are mollusks in which the **head** is well developed, the **foot** is typically broad and flattened, muscular, and adapted for creeping, and the **visceral mass** is commonly coiled upward in a spiral. The shell covers the visceral mass and usually exhibits a corresponding spiral configuration (Fig. 13.11). The apex of the shell is generally closed, and the lower end presents an expanded opening, the **aperture**, into which the head and foot may be completely retracted for protection. In many species this aperture may be closed by a horny or calcareous **operculum**.

The remote ancestors of the gastropods were evidently bilaterally symmetrical animals, possibly similar in general appearance to the modern amphineurans. As indicated by the anatomy and embryonic development of

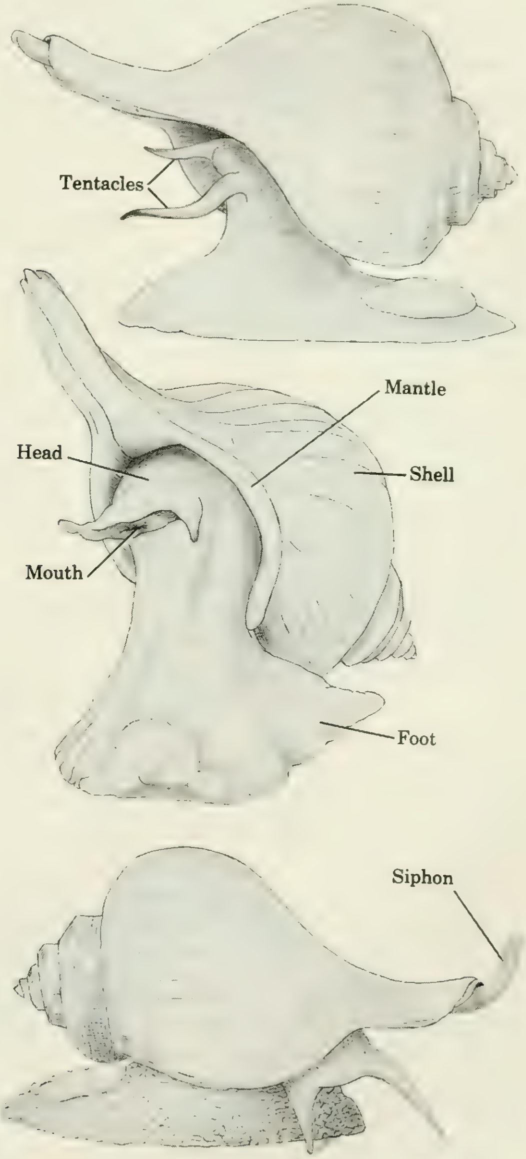


Fig. 13.11. The marine gastropod *Busycon canaliculatum* in positions assumed during locomotion. This large snail inhabits muddy bottoms, feeding on bivalves, and reaches a length of almost 1 foot. (Drawings by George T. Kline.)

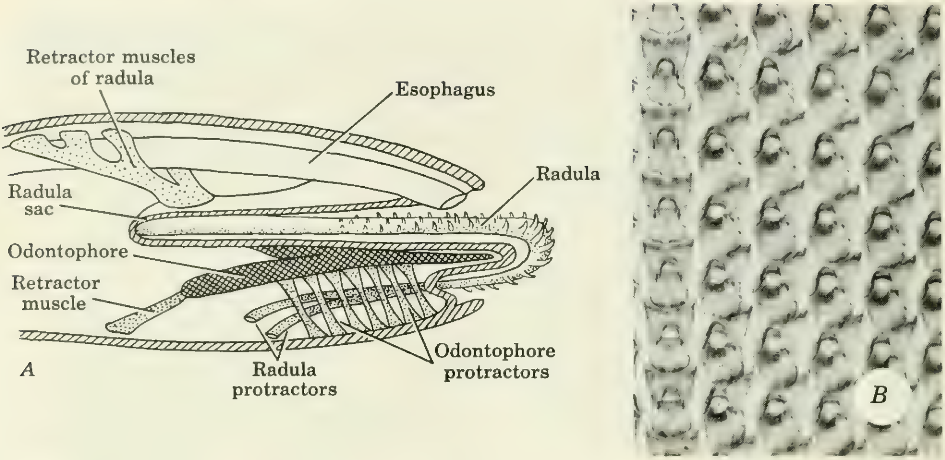


Fig. 13.12. The gastropod radula. *A*, radula of the snail *Busycon*, showing relationships of the muscles which operate it; diagrammatic. *B*, photomicrograph of the surface of the radula of a fresh-water snail. (*A*, redrawn from M. Pierce in F. A. Brown, Jr., *et al.*, *Selected Invertebrate Types*, copyright 1950 by John Wiley and Sons, Inc., printed by permission; *B*, photograph courtesy General Biological Supply House, Inc.)

snails, two fundamental changes have occurred in the course of their evolution. One of these developments involved a dorsal elongation and flexure of the visceral mass, eventually accompanied by spiral coiling. This has resulted in the production of the characteristically coiled, elongated visceral hump of most snails, containing part of the **intestine**, the **digestive diverticulum**, and the **gonad**. The other process consisted of a rotation, or torsion, about the dorsoventral axis of the body. This brought the originally posterior **mantle cavity**, containing the gills, the anus, and the openings of the excretory and reproductive ducts, around to lie anteriorly above the head, in some cases, or to an anterolateral position. The evidence for the occurrence of this torsion is found in the consequent adjustments and alterations of internal anatomy, particularly as they have involved the nervous system. Such evidence also indicates that a certain amount of "detorsion," or reversal of rotation, has occurred in many forms whose ancestors had undergone complete torsion.

Some gastropods have shells which are not coiled; this probably represents a secondary condition, because the internal organs show evidences of coiling, and related species have somewhat coiled shells. An interesting type showing greater coiling in the visceral mass than in the shell is represented by species of the genus *Crepidula*, the "boat shells." These are sedentary snails which feed by the use of cilia and sheets of mucus. This method of feeding is unusual among gastropods, most of which use the tongue-like **radula** (Fig. 13.12). This organ consists of a ribbon of tissue bearing rows of horny teeth; by the operation of a complicated arrangement of specific muscles, this ribbon is protracted, drawn upward against the food mass, and retracted. The particles of food rasped away by the teeth are then ingested. Some carnivorous snails use the radula to drill holes in the shells of bivalves on which they feed.

The marine gastropods also include an interesting group known as Nudibranchia, which, as indicated by the name, have exposed gills. In these snails the adult is without a shell (Fig. 13.13). The gills of nudibranchs are not homologous with those of other gastropods but are secondarily developed projections from the dorsal surface of the body. The young nudibranch has a spirally coiled shell which is lost during growth to maturity, as the dorsal part of the visceral mass assumes a bilateral symmetry. Internally, however, the anatomy of the adult animal retains a coiled condition. Nudibranchs are often large, up to 6 inches in length, and some exhibit spectacularly brilliant coloration. Two other small divisions of the marine gastropods, the Pteropoda and Heteropoda, contain many species that are without external shells. These animals are pelagic, swimming actively in the open sea by means of a highly modified foot.

In all the marine gastropods the primary organs of gaseous exchange are the gills, with the mantle often serving as an accessory in this function. Although eminently suitable in an aquatic environment, gills are impractical on land. The terrestrial gastropods, doubtless descended from aquatic ancestors, have lost the gills of their forebears and have replaced them with **lungs**. Air is drawn into the mantle cavity, and the mantle itself, which is richly vascularized in these forms, serves as the site of gas exchange. Many fresh-water snails "breathe" in this fashion and are presumably descended from terrestrial forms, just as aquatic mammals such as the seal are presumed to have evolved from terrestrial ancestors. The land slugs, of which *Ariolimax* is a representative genus, are a modified type of terrestrial snail in which the shell persists as a vestige embedded in the dorsal wall of the body (Fig. 13.14). Terrestrial and fresh-water air-breathing snails,

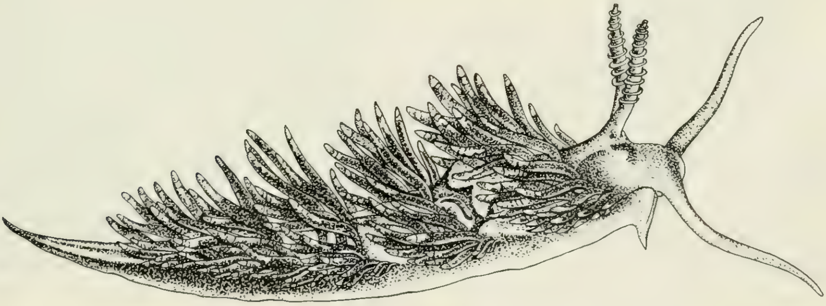


Fig. 13.13. A nudibranch gastropod, *Eolis coronata*. The numerous dorsal projections are the cerata, or gills. (Redrawn from J. Alder and A. Hancock, 1846, *Monograph of British Nudibranch Mollusca*, Part 2.)

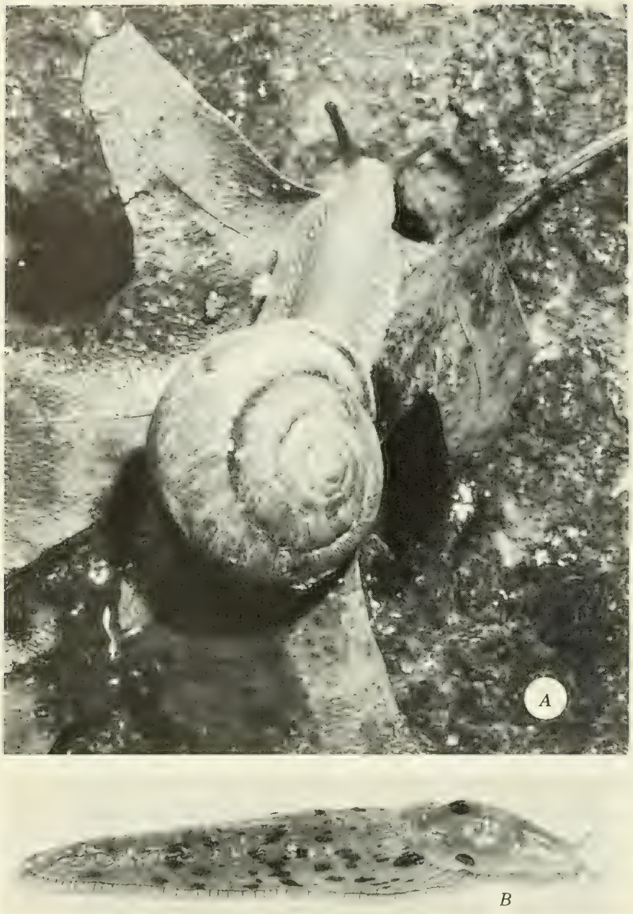


Fig. 13.14. Pulmonate gastropods. *A*, *Polygyra*, a terrestrial snail; note the characteristic spiral growth pattern of the shell and the successive lines of growth marking periodic additions to the edge of the shell. *B*, a giant land slug, *Ariolimax columbianus;* the actual length of this specimen was more than 6 inches. The saddle-shaped remnant of the shell and the opening through which air enters the mantle cavity can be clearly seen. (*A*, photograph courtesy The *Missouri Conservationist; B*, from A. R. Mead, 1943, *American Midland Naturalist*, vol. 30, reprinted by permission of the author.)

including the slugs, are called **pulmonate** gastropods; the marine and fresh-water forms possessing gills are termed **branchiate** gastropods.

In most gastropods the sexes are separate, but some species are monoecious. The eggs, laid in capsules or in gelatinous masses, contain sufficient yolk to sustain the developing individuals until they reach the stage of hatching. In fresh-water and terrestrial forms the young appear as miniature adults; in many marine snails, the sequence includes free-swimming **trochophore** and **veliger** larvae.

The Gastropoda illustrate particularly well the diversity of structure and habitat attained by the Mollusca. Their ancestral home seems to have been the ocean, since the more primitive types are marine, whereas the more specialized forms occur in fresh water and on land. It appears that from the marine environment some penetrated into fresh water, and some invaded the land, becoming adapted to these new habitats. The pulmonate fresh-water snails are apparently descendants of land snails which returned to an aquatic habitat. Other descendants of the primitive, creeping marine gastropods took to a pelagic life in the open ocean and gave rise to the existing pteropods and heteropods.

THE CLASS SCAPHOPODA

The mollusks belonging to this class are characterized by dorsoventral elongation, without spiral coiling, and by a simple, unbranched foot adapted for burrowing. The body is covered by a shell which is slightly curved and resembles a miniature tusk. The shell is open at both ends; the foot, together with several oral tentacles, protrudes from the ventral end, which also contains the incurrent opening into the mantle cavity. The dorsal end bears the

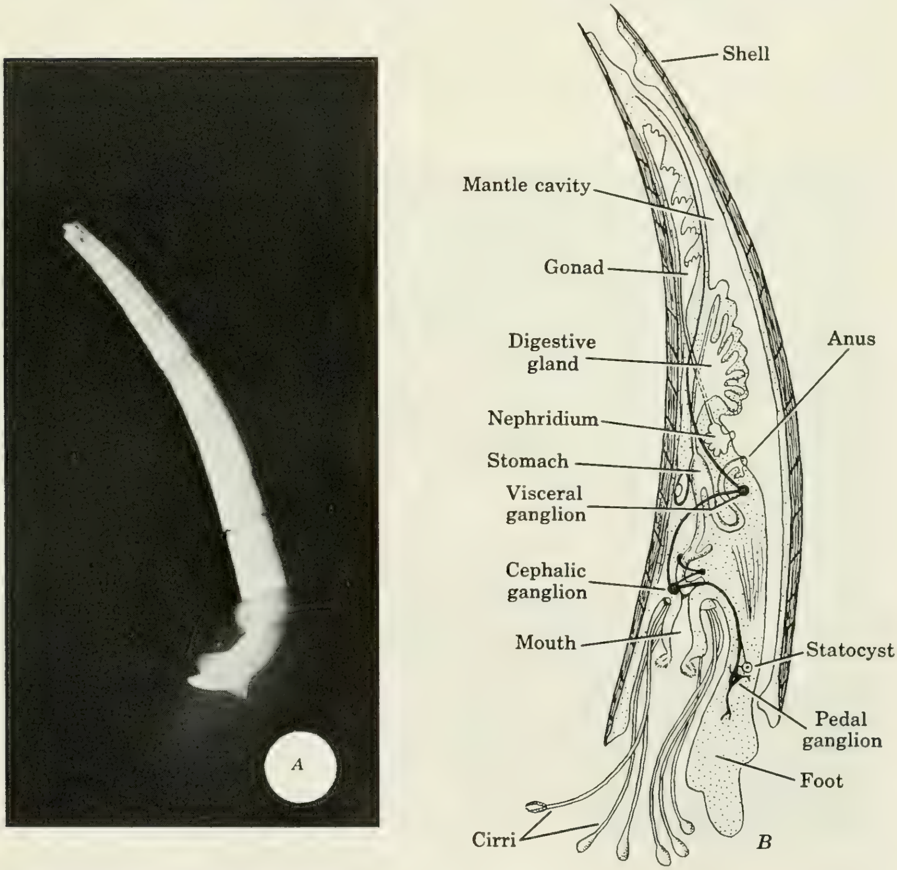

A
Shell
Mantle cavity
Gonad
Digestive gland
Anus
Nephridium
Stomach
Visceral ganglion
Cephalic ganglion
Mouth
Statocyst
Pedal ganglion
Foot
Cirri
B

Fig. 13.15. Class Scaphopoda: *Dentalium entale*. *A*, photograph of a preserved specimen, lateral aspect. *B*, semidiagrammatic longitudinal section to show general internal organization. (*A*, photograph by Bassett Maguire, Jr.; *B*, redrawn from W. Stempell, 1926, *Zoologie im Grundriss*.)

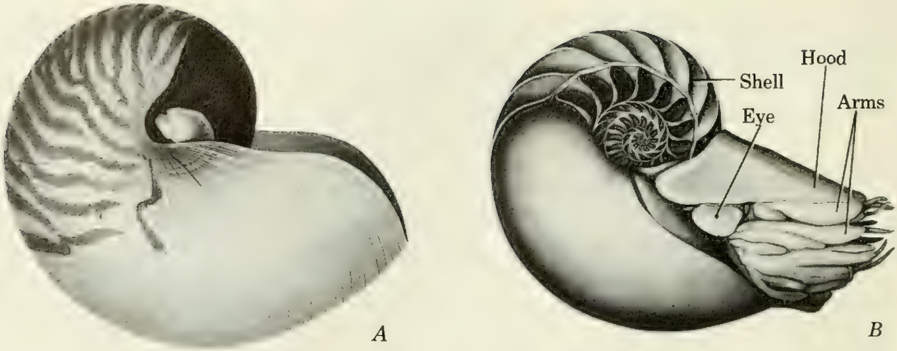


Fig. 13.16. The pearly nautilus, *Nautilus pompilius*. *A*, lateral view of an empty shell. *B*, an animal from which the right half of the shell has been removed; the exposed surface of the body within the large chamber is the mantle. (Reproduced from L. E. Griffin, 1900, *Memoirs of the National Academy of Sciences*, vol. 8.)

excurrent channel leading from the mantle cavity. The general structural features of a representative scaphopod, *Dentalium entale*, are shown in Figure 13.15.

THE CLASS CEPHALOPODA

The cephalopods are mollusks in which the visceral mass is much elongated dorsoventrally, and in which the foot is subdivided into numerous flexible, muscular arms or tentacles bearing rows of adhesive cups. The class includes the squids, cuttlefishes, octopi, and nautili, all of which are among the most highly developed types of mollusks. The giant squids, for example, attain a size unmatched by any other invertebrate animal; one recorded specimen had a body 18 feet long, with 34-foot arms. The class is subdivided into the **Tetrabranchiata,** with external shells, many arms, no ink sac, and two pairs of gills; and the **Dibranchiata,** with internal shells or none, fewer arms, an ink sac, and one pair of gills. The tetrabranchiates include a very large number of extinct species, the nautiloids and ammonoids (see Fig. 20.4, p. 624). The ammonoids were a conspicuous type of marine life during the Mesozoic Era (ended about 60,000,000 years ago), but there are no living representatives of this group. The nautiloids, once flourishing in the past, have only one modern representative, the genus *Nautilus* (Fig. 13.16). The nautilus, like the brachiopod *Lingula* (p. 363), is a primitive and long-persisting type; it now has a very limited geographical range, being found only in the tropical Pacific and Indian Oceans.

The dibranchiates include all other living cephalopods. A familiar example is the squid, *Loligo pealeii* (Fig. 13.17); a brief discussion of structure and function in this animal will serve for cephalopods generally. The tapered, cylindrical body of the squid is almost entirely covered externally by the **mantle,** which has a tough, rubbery texture and is very muscular. At what appears to be the posterior end of the animal a pair of horizontal **fins** extend laterally; the **tentacles** lie at the opposite end. The mantle encloses a **mantle cavity,** a space which surrounds the **visceral mass** and contains the paired, feathery **gills.** Attached to the visceral mass at the open end of the mantle cavity is the exposed portion of the body, comprising the combined **head** and **foot.** The foot is represented by the ten sucker-bearing **arms** and by the **siphon,** a nozzle-like structure protruding from the mantle cavity. The head bears the **mouth,** surrounded by the arms and provided with a pair of horny **jaws.** On the sides of the head are located the large and well-developed **eyes.**

The visceral mass contains the **digestive tract,** which is essentially U-shaped (Fig. 13.18). A long **esophagus** leads from the mouth to the **stomach;** the stomach is connected with a large, sac-like **caecum** and receives the ducts from two **digestive glands.** From the point where the caecum joins the stomach, the **intestine** extends forward, becoming the **rectum** which opens into the mantle cavity at the **anus.** The conspicuous **ink sac** opens into the rectum.

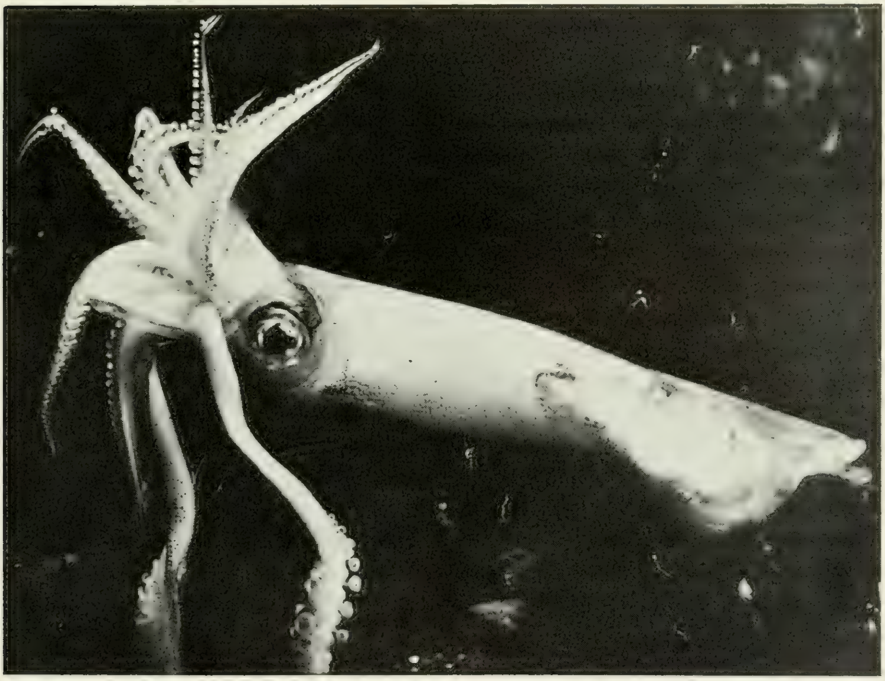


Fig. 13.17. The common squid, *Loligo pealeii.* Note the eight short tentacles and two longer ones, all provided with rows of suction cups, and the highly developed eyes. The photograph shows the chromatophores in the skin, which by continually expanding and contracting change the color and appearance of the animal. (Photograph by George Lower.)

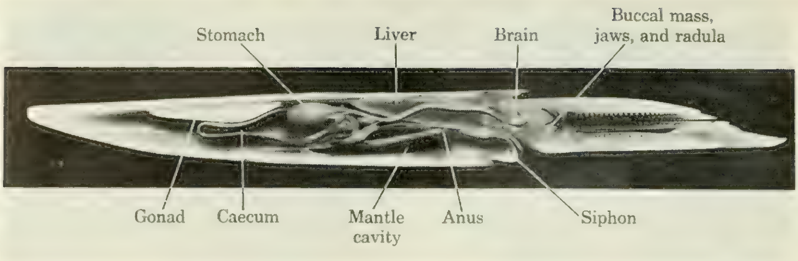


Fig. 13.18. The squid, *Loligo pealeii:* internal anatomy as shown by a sagittal section of the body. (Photograph of a model, courtesy American Museum of Natural History.)

The **circulatory system** is remarkably well developed in comparison with that of other mollusks (Fig. 13.19). The large, median **systemic heart** gives off an **anterior** and a **posterior aorta,** whose branches are distributed among the organs. Symmetrically placed anterior and posterior collecting vessels conduct blood from the tissues to a pair of **branchial hearts,** accessory pulsatile organs lying at the bases of the gills. These hearts propel blood through the vessels of the gills and into the systemic heart for redistribution. The cephalopod vascular system is noteworthy in that it is a **closed system** with **capillaries,** in contrast to the open systems of other mollusks.

The **excretory organs** are a pair of large, glandular **nephridia** lying just below the heart. These structures are richly vascularized and apparently remove wastes from the circulating blood. They open into the mantle cavity at a pair of **nephridiopores.**

Squids are dioecious. The large **gonad** occupies a major portion of the posterior end of the visceral mass, and the gametes are conducted to the outside through a complex series of ducts with specialized accessory glands. In the male the spermatozoa are formed into bundles, or **spermatophores,** which at the time of mating are transferred into the mantle cavity of the female. Fertilization occurs in the oviduct, and the zygotes are embedded in fingerlike, gelatinous masses which are extruded and attached to the substratum. The egg of the squid contains a large amount of yolk, and the young animal hatches as a miniature adult able to swim and capture food.

The **nervous system** of the squid can be correlated with the typical molluscan plan, but it is very highly developed and specialized. It centers in a large ganglionic mass, the **brain,** lying in the head and enclosed by a cartilaginous endoskeleton. The brain probably represents the basic three pairs of ganglia, as found in other mollusks, but it has been shown that the brain of the squid contains specialized areas devoted to **sensory, motor,** and **associative** functions. Nerves radiate from the brain to all parts of the body. One pair of large nerves connects the brain with a pair of **stellate ganglia** on the inner surface of the mantle, and from these ganglia nerves are distributed to the muscular tissues of the mantle. The highly specialized **eyes** lie near a pair of large **optic ganglia**, from which **optic nerves** enter the brain.

The entire organization of the squid is thus that of an active, predaceous animal. Aside from the cartilaginous brain case, the skeleton consists only of a light, proteinaceous, leaf-like **pen** enclosed within the tissues of the mantle on the apparently dorsal side of the body. This may be contrasted with the more massive calcareous shells of the nautilus and of the extinct tetrabranchiates. When not moving rapidly through the water, the squid maintains a continuous pumping action of the mantle, drawing water into the mantle cavity and expelling it through the siphon. These same pumping movements are utilized in swimming; the animal moves backward or forward with great rapidity, direction being determined by adjustment of the siphon. The fins and tentacles are used as stabilizers and steering devices. In escaping predators, the squid may release a stream of "ink" from the rectum; this

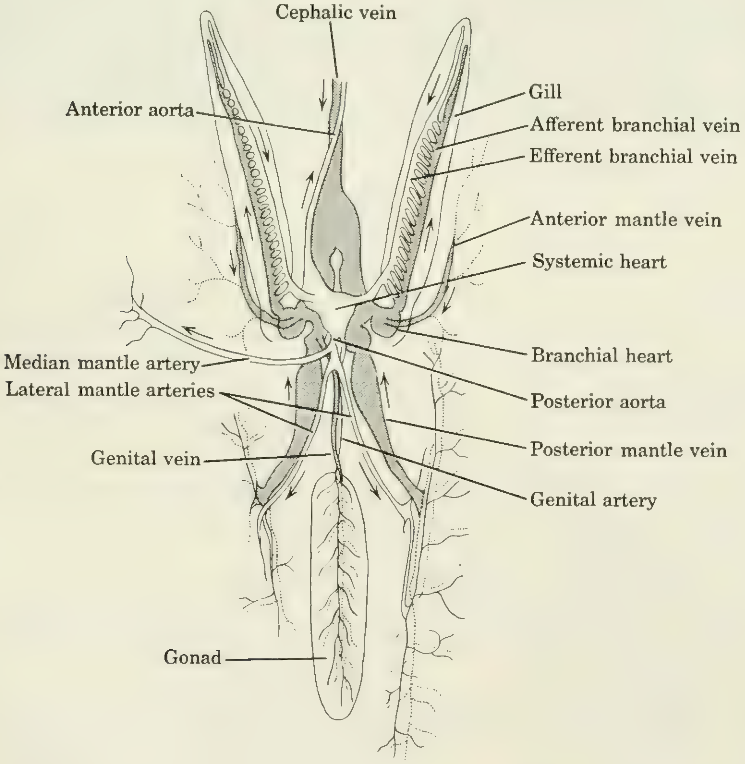

Cephalic vein
Gill
Anterior aorta
Afferent branchial vein
Efferent branchial vein
Anterior mantle vein
Systemic heart
Branchial heart
Median mantle artery
Lateral mantle arteries
Posterior aorta
Posterior mantle vein
Genital vein
Genital artery
Gonad

Fig. 13.19. Major features of the circulatory system of the squid. Vessels carrying oxygenated blood are clear; those carrying blood that has lost its oxygen to the tissues are stippled. Note the branchial heart at the base of each afferent branchial vein, functioning to increase pressure and velocity of blood traversing the gill. Compare this system with that of a bivalve, shown in Figure 13.3, p. 374. (Adapted from L. W. Williams, *Anatomy of the Common Squid*, Leyden, 1909.)

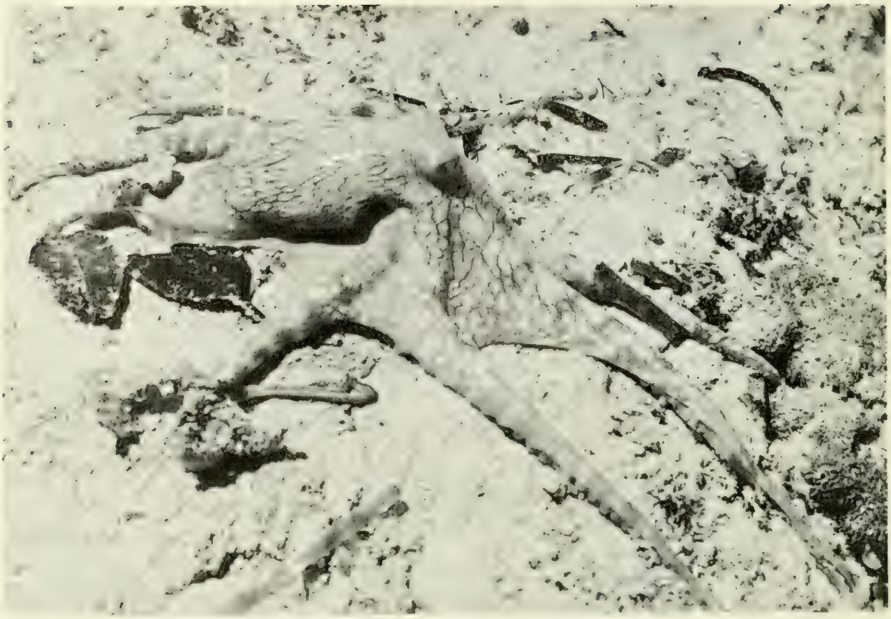


Fig. 13.20. An octopus. (Photograph by John F. Storr.)

deeply pigmented fluid stains the water being pumped from the mantle cavity and spreads to hide the movements of the squid. In feeding, the animal depends on its great speed and agility to capture fish, which are grasped in the arms and brought to the mouth. Here, the beak-like jaws cut off coarse pieces of the prey, which are passed into the stomach and caecum for digestion. It is interesting to note that the squid bears in the floor of the buccal cavity a vestigial **radula** resembling the feeding organ of chitons and of gastropods. In fact, radulas occur in all the modern molluscan classes except the pelecypods.

The greater efficiency and higher specialization of the circulatory and sensory-neuro-muscular systems of the squid are presumably related to its more active way of life, as compared with the more sedentary representatives of other molluscan classes.

Other dibranchiates are the giant squids, which inhabit the ocean far from land but are occasionally washed ashore; the cuttlefish, *Sepia*, known for its pigment and for its shells, which are the light, calcareous "cuttlebones" sold as bill sharpeners for cage birds; the "devil fish," *Octopus*, a less active animal than the squid, with eight arms and no vestige of a shell (Fig. 13.20); and the paper nautilus, *Argonauta*. The paper nautilus builds a very thin and fragile spiral shell, resembling in form that of the nautilus, but this shell is used chiefly as an egg case and does not enclose the body of the adult.

The Mollusk Body Plan

The primitive, generalized ancestor of the modern mollusks was probably an animal with a simple head bearing the mouth, and with a body consisting of a flattened foot surmounted by a visceral mass containing the organs (Fig. 13.21). The visceral mass, we may assume, was covered dorsally by a shell lined by a mantle. Within a posterior cavity enclosed by the overhanging mantle were a pair of gills and, near the anus, the paired openings of nephridia and reproductive organs. The visceral mass probably contained a small coelom, a pair of digestive glands, a pair of nephridia, an open circulatory system, a pair of reproductive organs, and a nervous system composed of three pairs of ganglia with their connectives. The characteristics of the fossilized shells of some of the earliest known mollusks, dating from the Cambrian (see Fig. 20.1, p. 617), are in agreement with such an interpretation of the features of forms ancestral to modern types. Although the soft parts of these ancient mollusks are unknown, their characteristics may be inferred from the features of the shells, muscle scars, etc.

The fundamental characteristics of the ancestral type are retained to some degree in all the modern descendants of this generalized ancestor. The phylum Mollusca exemplifies particularly well the **principle of adaptive radiation**, which leads to the production of a number of distinct types, through evolution in different directions from a primitive stem form. Each type so produced is generally adapted to the conditions of life in a particular type of habitat. Thus the chitons are little modified in their general features; the pelecypods have become bivalved and laterally compressed in adaptation to a burrowing existence. The elongated scaphopods represent a different set of adaptations to burrowing life. The gastropods have undergone innumerable

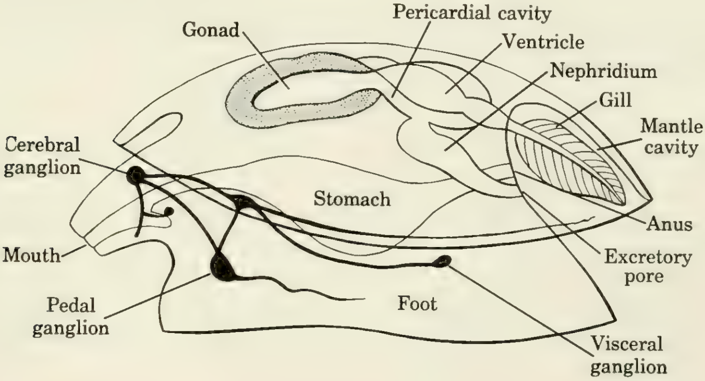


Fig. 13.21. Hypothetical ancestral type showing features which may have been characteristic of the forms from which all mollusks have evolved by adaptive radiation. (Redrawn from P. Pelseneer in E. Ray Lankester, *A Treatise on Zoology*, Part 5, 1906.)

modifications in adjusting to a variety of habitats; the visceral mass has become coiled and rotated, and sometimes secondarily uncoiled and unwound, but for the most part the gastropods have retained the flattened foot adapted to creeping. The cephalopods have evolved in adaptation to an active, free-swimming, predaceous existence. Yet in all of these highly modified and generally successful types, we can still trace the basic plan of organization of the ancient ancestral mollusk.

One of the peculiar and somewhat puzzling features of the molluscan body plan is the absence of segmentation at any stage. This is the more striking when mollusks are compared in this respect with members of the phylum Annelida, to which we shall devote our attention in the next chapter. Annelids and mollusks have obviously descended from a common ancestry; their cleavage patterns, larval types, general level of organization, and other features are very similar. Yet molluscan larvae transform into the adult condition without showing a trace of segmentation, whereas the larvae of annelids begin very early to develop the serial repetitions of parts characteristic of the phylum.

A rather startling recent report may be interpreted as indicating that mollusks were not always unsegmented, and perhaps as revealing a stage in the evolution of the body plan of modern forms. A new species of limpet-like mollusk has been dredged from the deep Pacific waters off the coast of Mexico; externally it presents many interesting features and resembles most closely a group of mollusks previously known only from fossilized shells dating from the Cambrian and somewhat later. This new species, *Neopilina galatheae*, thus takes its place among the "living fossils" (see p. 630). Its availability makes possible a study of the internal anatomy of primitive types about which only what could be inferred from the characteristics of the fossil shells was known previously. Preliminary studies on *Neopilina* have revealed a well-developed internal segmentation, involving coelom, nephridia, gonads, heart, and other structures. Students of the Mollusca are eagerly awaiting the results of detailed anatomical studies, which promise to add new perspective to our views on molluscan evolution.

CHAPTER 14

CHAPTER 14

SEGMENTED WORMS:

The phylum **Annelida** is the second major group of animals possessing a true coelom formed in the schizocoelous manner (p. 368). The annelids are elongate worms whose most conspicuous characteristic is the relatively unspecialized segmentation found in most species. The name of the phylum is derived from the Latin *annulus* ("little ring") and refers to the ringed appearance which the serially repeated segments give to the body. In all annelids there is some differentiation at the two ends, but the main part of the body is composed of segments which are usually of similar structure internally as well as externally. Other annelid characteristics include the extensive coelom, separated into segmental compartments by transverse partitions, or septa; paired segmental excretory organs, the nephridia; and the ventral nerve cord composed of paired ganglia at segmental intervals, connected anteriorly with the dorsal "brain" by a pair of circumpharyngeal connectives.

The annelids, with various other animal forms, were long classified in a phylum called the Vermes. Now, however, in recognition of their specific distinguishing characteristics, the annelids are considered as a separate major phylum. The phylum Annelida comprises four classes: the class **Archiannelida,** a miscellaneous collection of primitive or secondarily simplified marine annelids; the class **Polychaeta,** chiefly marine annelids with many bristles, or **setae;** the class **Oligochaeta,** which includes the earthworms and many small annelids of fresh water, with bristles few in number; and the class **Hirudinea,** the leeches.

Annelids are typically animals that burrow or crawl upon the bottom in the ocean or in fresh water. Some are free-swimming, at least during the breeding season, and others are adapted to life in moist soil. Many marine species build permanent tubes which they inhabit; in other species the tube is temporary, like a burrow, and may be abandoned for another. Some annelids are actively predaceous, seizing their prey in well-developed jaws; others, notably the permanently tube-dwelling polychaetes, feed upon microscopic particulate matter brought in by ciliated tentacles or entrapped in sheets of mucus.

The fossil record of evolution among annelids is meager indeed, being limited to relatively few complete animals but featuring numerous hard parts, such as chitinous jaws and calcareous tubes, as well as innumerable "worm

The Phylum Annelida

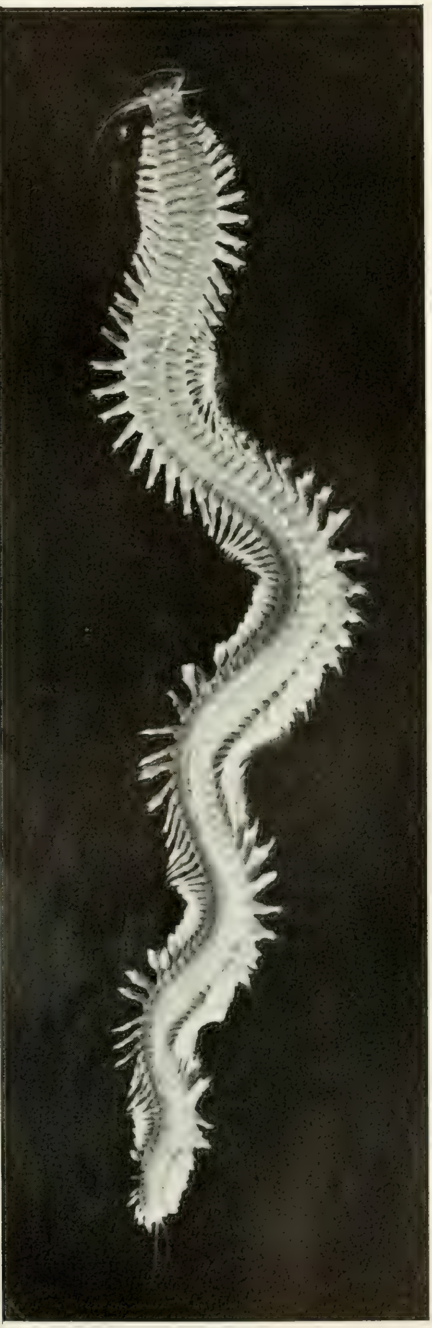


Fig. 14.1. The clamworm, *Nereis virens*, in locomotion. The parapodia beat in coordinated strokes; note also that in each short region the positions of the parapodia are related to the way in which the body is bent. (Photograph by Bassett Maguire, Jr.)

tracks" from the mud flats of ancient seas. The earliest fossil annelids date from the Cambrian period (roughly 500 million years old) and indicate that considerable differentiation had already taken place at that time.

There are few annelids in which the size of the individual exceeds that of the average earthworm. Their economic significance is not great, except as they form an integral part of the food supplies of larger aquatic animals, as well as of birds and mammals. Of more direct importance to man is the activity of earthworms in improving soil texture. Populations of these worms may exceed 50,000 per acre, and they tunnel through and turn over the soil very effectively.

For comparative studies of animals, the annelids are important because of their simple metameric structure. The present chapter describes the clamworm and the earthworm as representative annelids, with particular attention given to the earthworm. This animal exhibits a structural and functional organization which may be considered intermediate in complexity between that of the hydra and that of the vertebrate.

The Class Polychaeta

The name Polychaeta ("many bristles") is appropriate for members of this class, the typical polychaete having on each segment a pair of appendages stiffened and fringed by many bristle-like structures. The polychaetes are almost exclusively marine forms and are abundant in all the oceans. According to the species, they are found crawling or burrowing upon the bottom, or inhabiting secreted tubes, or even swimming freely at the surface. The earliest annelid fossil remains are of worms recognizable as polychaetes. Taken as a whole, the polychaetes best typify the annelid level of organization; they include generalized forms as well as many that are highly specialized.

The Clamworm: *Nereis virens.* As well as any species that can be selected, the clamworm represents the polychaetes and the entire phylum (Fig. 14.1). This animal lives just below low-water mark in sand and fine gravel, or under stones, without forming permanent burrows. When free in the water, it swims effectively by lateral undulations of the body, assisted by the paddle-like appendages; at other times it creeps on the substratum, "walking" on its segmental appendages. The animal customarily burrows into the bottom, lying with only the head exposed. The **mouth** opens ventrally at the anterior end and is encircled by the first somite, the **peristomium.** The dorsal surface of the head region is well equipped with numerous sense organs in the form of **eyes, tentacles,** and **palps** (Fig. 14.2). The **anus,** flanked by two **anal cirri,** which are tactile organs like the tentacles of the head, lies at the extreme posterior end. The body is composed of **somites,** each bearing a pair of paddle-like **parapodia,** which are the organs of locomotion and gaseous exchange. Each parapodium consists of dorsal and ventral leaf-like lobes, the dorsal being the larger. Toward the anterior end of the body the parapodia are reduced in size; and toward the posterior end, where new somites are added as the worm grows, they are not fully developed. Parapodia are found on all segments except those surrounding the mouth and the anus. *Nereis* is thus composed of a series of similar structural units repeated throughout the body, but with certain specializations at each end.

Internally, the **digestive tract** is a straight tube extending from mouth to anus. The **buccal region** and **pharynx** are eversible, and the pharynx, bearing two **jaws** and numerous small **denticles,** constitutes a **proboscis** used in seizing prey. A narrow **esophagus,** receiving ducts from a pair of glands, follows the pharynx; from about the twelfth somite posteriorly, the tract consists of a simple tube, the **stomach-intestine.** Surrounding the digestive tract is a well-defined coelomic body cavity, divided by septa extending transversely from body wall to gut. The compartments thus formed constitute the **coelom;** they are further divided into lateral halves by **mesenteries** which extend in the median plane dorsal and ventral to the gut. The coelomic cavities contain a fluid with amoeboid cells, comparable with the lymph of a vertebrate.

The **circulatory system** is of the "closed" type, consisting of a dorsal and a ventral longitudinal blood vessel, with lateral branches to capillary beds in the body wall and the wall of the intestine. Capillaries are particularly numerous

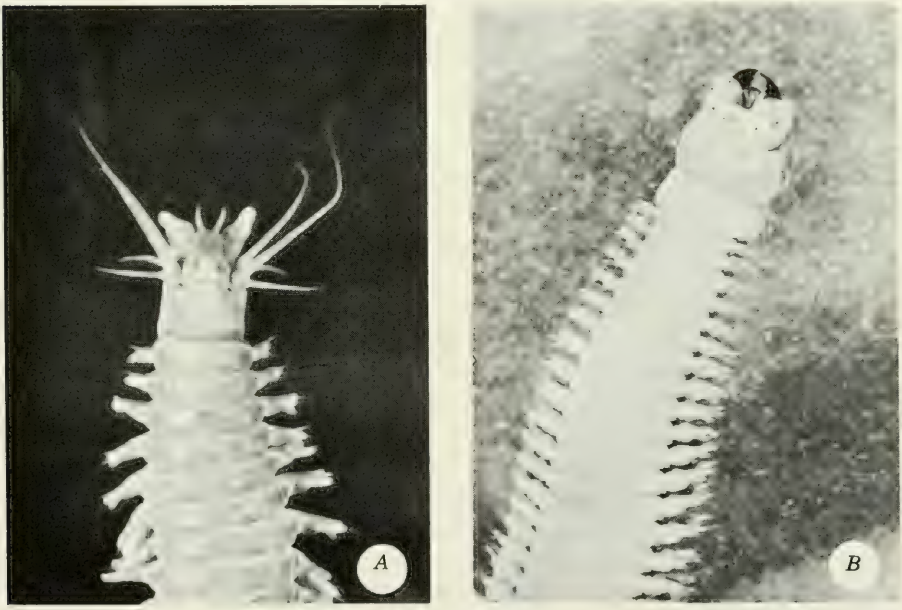


Fig. 14.2. Specializations of the anterior end of *Nereis virens*. *A*, dorsal view; note the two prostomial and eight peristomial tentacles, the two blunt palps, and the eyes. *B*, ventral view of a specimen with pharynx and jaws everted, as in seizing prey. (Photographs by Bassett Maguire, Jr.)

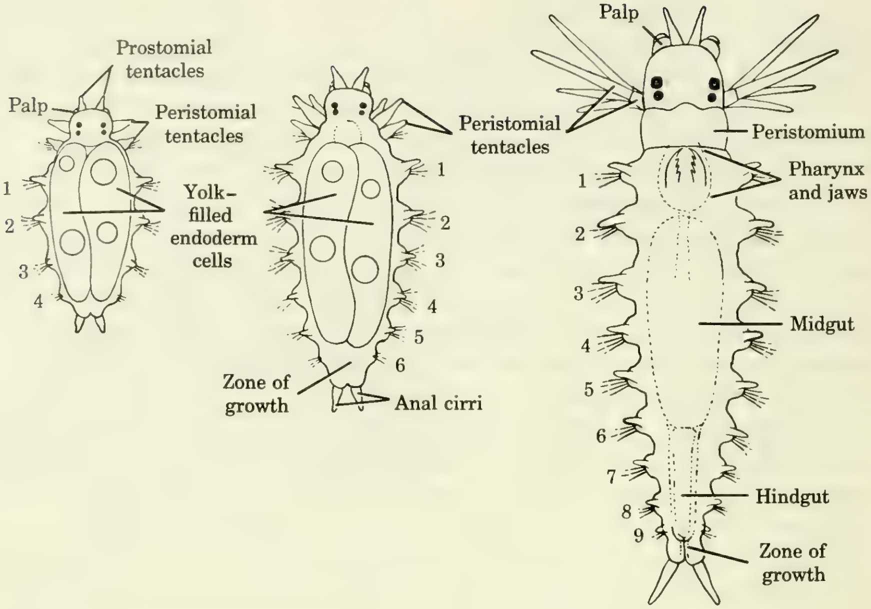

Prostomial tentacles
Palp
Peristomial tentacles
1
2
3
4
Yolk-filled endoderm cells
Peristomial tentacles
1
2
3
4
5
6
Zone of growth
Anal cirri
Palp
Peristomium
Pharynx and jaws
1
2
3
4
5
6
7
8
9
Midgut
Hindgut
Zone of growth

Fig. 14.3. Early developmental stages of *Nereis dumerilii*. The earliest free-swimming stage in this form is not a trochophore (cf. *Polygordius*, Fig. 14.17, p. 418) but a larva with a head and the beginnings of segmentation. In subsequent stages, note the successive addition of segments at the posterior end, and the progressive modification of the first segment into the peristomium (cf. Fig. 14.2). (Redrawn from F. Hempelmann, 1911, *Zoologica*, vol. 25.)

in the thin dorsal lobes of the parapodia; these dorsal lobes serve as gills. The movement of blood within the vascular system is effected by peristaltic contractions of the larger vessels, particularly of the dorsal vessel. In the living worm, pulsations can be seen passing from posterior to anterior in this vessel. The blood is colored red by the respiratory pigment **hemoglobin,** which in these worms is dissolved in the plasma, not contained in blood cells as in a vertebrate (see p. 63). The **excretory organs** are paired **nephridia,** found in all somites except those near the ends of the body. Each nephridium is a tube, opening at one end into the coelom and at the other end passing through the body wall and opening to the exterior. The inner end bears a ciliated funnel, the **nephridiostome,** and the tube itself is lined in part by ciliated epithelium. It is believed that waste products of metabolism are collected from the coelomic fluid by these organs and so eliminated from the body.

The **nervous system** represents the typical annelid plan, consisting of a pair of ganglia, the **brain,** located dorsally in the head region and connected around the pharynx with the first of a series of ganglia making up the **ventral nerve cord.** Nerves and nerve fibers radiate from the ganglia to innervate muscles and sense organs and also to connect with parts of a subepidermal plexus layer. The nerves are similar in number and distribution in all the somites, with the exception of those at the anterior end. There is thus a metameric repetition of parts in the nervous system as in other systems.

Nereis is dioecious, as are most polychaetes. The **ovaries** and **testes** are not permanent organs but are formed anew at each breeding season by the differentiation of cells lining the coelomic cavities. In some polychaetes these developments are limited to the posterior portions of their bodies. At a specific time in the breeding season, these detach from the anterior ends, swim to the surface of the sea, and congregate in great swarms. Ova and spermatozoa are emitted in astronomical numbers during these swarming periods, either through the nephridia or by rupture of the body wall, and fertilization occurs in the sea water. In many polychaetes the zygote develops into a ciliated larva, the **trochophore** (see Fig. 14.17, p. 418). After a period of free-swimming existence this larva seeks the bottom and transforms into a young adult, with a relatively large head region and only a few so-called "primary" somites. Subsequent growth involves the addition of successive new somites at a region just anterior to the segment bearing the anus (Fig. 14.3). This mode of growth, by the addition of "secondary" somites posteriorly, is to some degree characteristic of all annelids. It is interesting, and possibly significant, that in the generalized polychaetes only the secondary somites are capable of producing gonads and gametes. This has given rise to the theory that the long, many-segmented bodies of these worms originally developed as an adaptation for the increase of reproductive capacity.

Other Polychaetes. In one of the older classifications the polychaetes were divided, on the basis of their mode of life and correlated structural organization, into the **Errantia**, or wandering forms, which are free-living like *Nereis*, and the **Sedentaria**, which are sedentary and live in tubes of somewhat more permanent construction. Although this distinction is rather too artificial to be of value in the taxonomic sense, it is still convenient in a brief consideration of the polychaetes. The worm *Amphitrite*, which is an example of the more or less sedentary forms, inhabits a mucus-lined tube in sandy or muddy bottoms. *Amphitrite* feeds upon microscopic organisms and particles of detritus, collected from the water by long, ciliated tentacles. *Pectinaria* (Fig. 14.4) builds a conical tube of sand grains cemented together by secretions. This tube is buried in the bottom or dragged about as the worm crawls. *Chaetopterus* is a large polychaete which excavates a permanent U-shaped burrow, lined by a parchment-like secreted layer and open at both ends to the water. The worm lies at the bend of the U, and by means of several pairs of large, fan-like parapodia maintains a current of water through the tube. The animal depends on this passing stream for oxygen, for the elimination of wastes, and for its food supply. Microorganisms are entrapped in a sheet of mucus, produced and manipulated by other highly modified parapodia.

In all of these sedentary forms the parapodia and the appendages of the

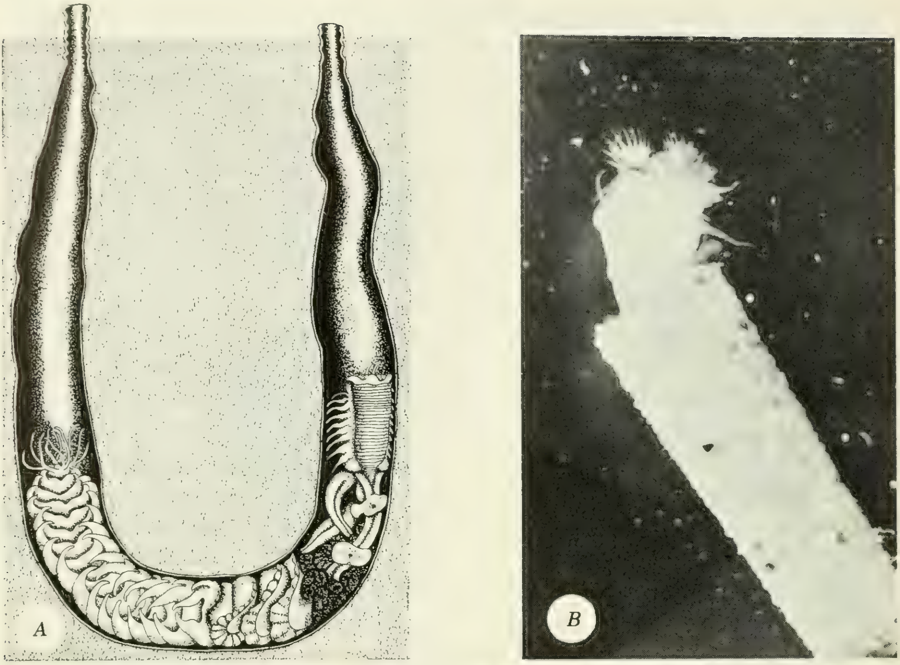


Fig. 14.4. Representative Polychaeta. *A*, *Chaetopterus* as it lies in its parchment-like tube; the fan-shaped parapodia maintain currents of water from which small particles of food are sieved by sheets of mucus. *B*, *Pectinaria gouldii;* the strong anterior setae are used in burrowing. Note the tube composed of sand grains cemented together. (*A*, redrawn with modifications from A. S. Pearse, 1913, *Biological Bulletin*, vol. 24; *B*, photograph by Charles Walcott.)

head region are modified in a variety of ways, in adaptation to the special requirements of their mode of life. In the errant forms like *Nereis*, however, the parapodia are usually essentially similar in structure and function throughout the length of the body.

The Class Oligochaeta

The name Oligochaeta ("few bristles") refers to the fact that the bristles of members of this class are scanty and often inconspicuous. In contrast to the polychaetes, which are predominantly marine forms, the oligochaetes are found almost exclusively in fresh water and in moist terrestrial environments. With the exception of the earthworms, most oligochaetes are small to minute in size.

The Earthworm: ***Habitat and General Activities.*** Earthworms are widely used in studies of the Oligochaeta because they are large enough for gross dissection and are abundant in most localities (Fig. 14.5). They are found in many parts of the world, even on isolated oceanic islands, wherever the ground is moist and the temperature sufficiently high. Locomotion is effected by extension and retraction of the body, aided by the setae. These bristles, presumably homologous with certain of the polychaete setae, can be withdrawn to reduce friction or protruded to catch against any surface with which the worm may be in contact. As the worm crawls, the movements of the setae in each region are coordinated with the movements of the body as a whole.

Earthworms burrow in the ground from a few inches to several feet beneath the surface. The burrows usually run straight down for several inches and then wind about irregularly, sometimes reaching a depth of 7 or 8 feet. In loose soil the worm burrows by forcing the pointed anterior end between the particles of earth. In soil of normal consistency the worm excavates the burrow by literally eating its way. The earth thus passed through the digestive tract of the worm is deposited on the surface of the ground as the feces, or castings, which are often seen in small piles where earthworms are abundant. In this manner lower layers of the soil are brought to the surface,

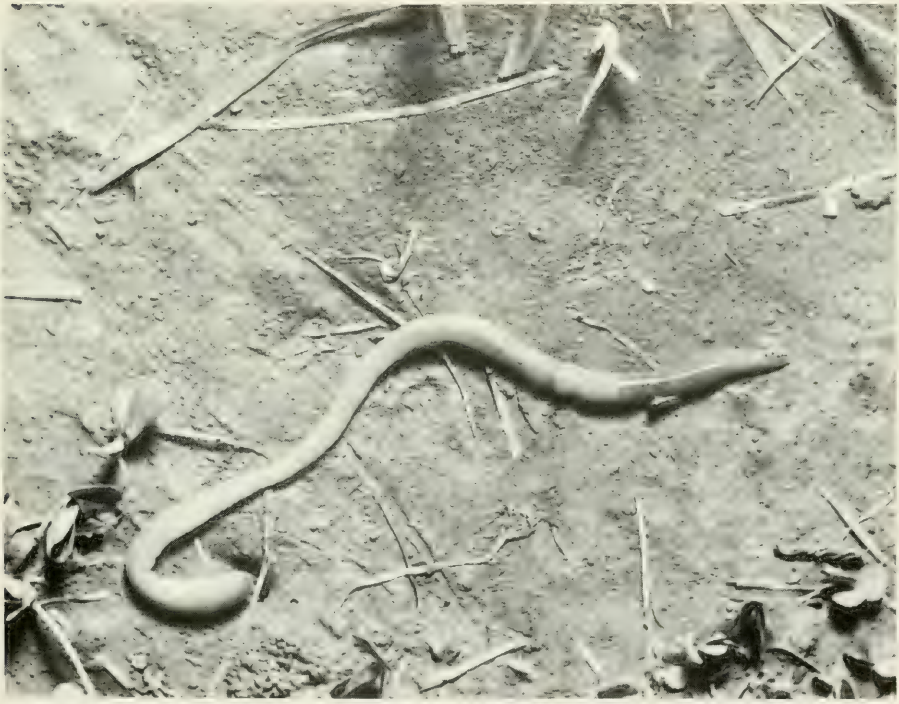


Fig. 14.5. An earthworm, *Lumbricus terrestris*, in a nocturnal exploration of the surface near its burrow. The anteroposterior differentiation in the body of the worm, and the specialized glandular region called the clitellum, are clearly shown (cf. Fig. 14.6). (Photograph courtesy *The Missouri Conservationist*.)

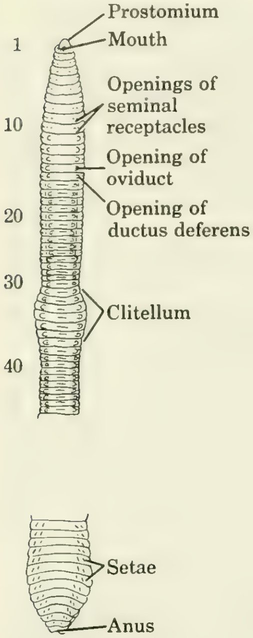


Fig. 14.6. Some external features of the anterior and posterior ends of the earthworm; ventral view. (From W. T. Sedgwick and E. B. Wilson, *General Biology*, copyright 1914 by Henry Holt and Co., reprinted by permission.)

and the effect upon the soil resembles that produced by turning with a plow. Earth which has passed through the worm's digestive tract is also modified chemically, and thus the tunneling activities of earthworms produce a twofold benefit to the soil.

Earthworms are nocturnal in their activities at the surface, although they sometimes appear in daylight after a shower. During the day they lie in the vertical part of the burrow near the surface, unless engaged in excavating at a greater depth. The mouth of the burrow is often closed by bits of grass or other materials drawn in at the finish of the night's activities. With the onset of darkness again, this plug is pushed aside, and the worm extends the anterior end of its body, exploring the surface in all directions but keeping the posterior end within the burrow. If disturbed, it can retract the exposed anterior end with surprising rapidity. When the soil is moist and atmospheric humidity high, earthworms secure most of their food at the surface. Leaves, bits of grass, and other plant materials are smeared with a saliva-like fluid and, thus softened, are nibbled away by the lips and swallowed. In times of drought, the worms avoid the surface and must depend on such nutrients as may be extracted from the soil that passes through the digestive tract in connection with their burrowing activities.

External Anatomy. The elongated, cylindrical body is bluntly pointed at both ends and is somewhat flattened or spatulate posteriorly (Fig. 14.6). The **mouth** is at the anterior end, surrounded by the first somite and overhung by a fleshy protuberance, the **prostomium.** The **anus** is a vertical slit-like opening in the last somite. The ventral side of the body is usually marked by a slight flattening, and its color is often lighter than that of the dorsal side. The somites—there may be 125 to 175 in a full-grown specimen of *Lumbricus terrestris*—are clearly separated from each other by intersegmental grooves. A swollen, girdle-like area of glandular epithelium, the **clitellum,** is usually located between somites 32 and 37; this secretes the egg capsules at the time of oviposition. Other glandular areas are found on certain anterior segments. The openings of the **ductus deferentes** (vasa deferentia), the male genital ducts, appear on the fifteenth somite as slit-like apertures surrounded by conspicuous lips. The openings of the **oviducts** are much smaller and are located on the fourteenth somite. In the grooves between segments 9 and 10 and 10 and 11 are the openings of the two pairs of **seminal receptacles.** The **nephridiopores,** openings of the nephridial tubules, which occur on each somite except a few at the anterior and posterior ends, are microscopic and variable in position. There are no structures resembling the polychaete parapodia, but on each somite there are four pairs of minute **setae.** These bristles, although small, are comparable with those found in the parapodia of *Nereis*. Openings leading from the coelom, called the **dorsal pores,** are located on the mid-dorsal line in the intersegmental grooves, except in the first 10 or 12 somites of the anterior end. The coelomic fluid can thus be exuded and spread over the surface of the body, presumably supplementing the slimy secretions of epidermal gland cells.

Structures and Functions Related to Metabolism. Internally, the structure of the earthworm resembles that of *Nereis*, although there are important differences. The **digestive tract,** which extends throughout the length of the body, is differentiated into a **buccal cavity,** a **pharynx,** an **esophagus,** a **crop,** a **gizzard,** and a **stomach-intestine** which extends posteriorly to the anus (Fig. 14.7). The buccal cavity and pharynx, strongly muscular, function in applying the suction by which the animal ingests food. The esophagus is a passageway, provided with well-developed **calciferous glands** between somites 10 and

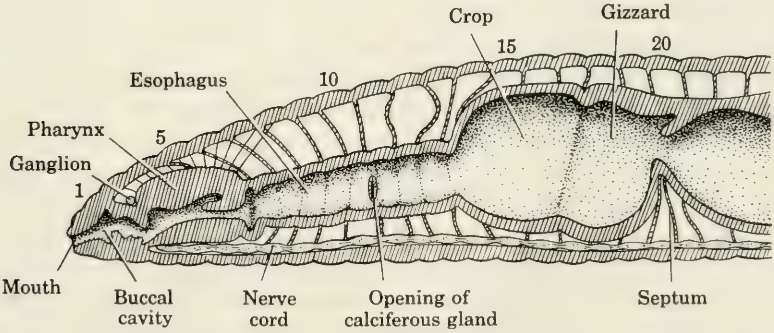


Fig. 14.7. Sagittal section of the anterior end of an earthworm; semidiagrammatic. (Modified from A. M. Marshall and C. H. Hurst, 1895, *Practical Zoology*.)

14. The size of these glands indicates an important function, but the role of their secretion is obscure. They produce spherules and concretions of calcium carbonate, which are emptied into the lumen of the esophagus. These may serve as a means of neutralizing excess acidity arising from ingested food, or as a mechanism of eliminating excess carbonate from the blood. The crop, as in other animals, is a storage place for food awaiting digestion; the gizzard serves to reduce the size of food particles. The stomach-intestine is the principal region of digestion and absorption. The surface area of this part of the digestive tract is increased significantly by the development of a continuous longitudinal fold, the **typhlosole**, which hangs down from the dorsal wall of the gut through the entire length of the stomach-intestine. **Absorption** involves the passage of products of digestion through the wall of the gut and into the blood vessels with which it is richly supplied.

The **coelom** of *Lumbricus*, like that of *Nereis*, is divided into successive compartments by transverse septa. These compartments are not completely isolated, however; in the median ventral part of each septum there is a large opening, which makes the coelom essentially a continuous cavity and permits the flow of coelomic fluid from one part of the body to another. In *Lumbricus* longitudinal mesenteries are not well developed, being limited to the mesentery which supports the blood vessel ventral to the gut.

The **circulatory system** is a surprisingly highly organized, closed set of vessels containing blood colored red by hemoglobin in solution in the plasma. The blood is circulated by peristaltic contractions in the walls of the larger blood vessels. The major features of the arrangement of the vascular system may be summarized as follows: two chief longitudinal vessels are present, the **dorsal vessel**, lying dorsal to the gut, above the typhlosole, and the **ventral vessel**, lying just beneath the digestive tube. In somites 7 to 11, these two vessels are directly connected by five pairs of so-called "hearts," which pass around the esophagus. One additional longitudinal vessel, the **subneural**, lies beneath the ventral nerve cord, bound up within its peritoneal sheath, and a pair of **lateral neural vessels** also parallel the nerve cord. The ventral vessel distributes blood to the nephridia, the body wall, and the wall of the gut, through specific branches at segmental intervals. From the body wall, blood may flow through collecting branches into the subneural and lateral neural vessels, to be sent to the dorsal vessel through paired, segmental **commissural vessels**. The commissural vessels also receive **parietal vessels** draining the body wall and **nephridial vessels** from the segmental excretory organs. From the gut wall blood reaches the dorsal vessel through numerous **dorsointestinal vessels**. The dorsal vessel, through which blood flows anteriorly, thus serves as a collecting vessel, although it sends blood to the gut wall through **afferent typhlosolar vessels**. The ventral vessel propels blood posteriorly, in general, and is the chief distributing vessel. In the region anterior to the "hearts" these relationships are reversed. Capillary networks lie in the tissues between adjacent branches of the distributing and collecting systems. Functionally, the blood flowing to all tissues nourishes their cells, brings oxygen to them, and removes

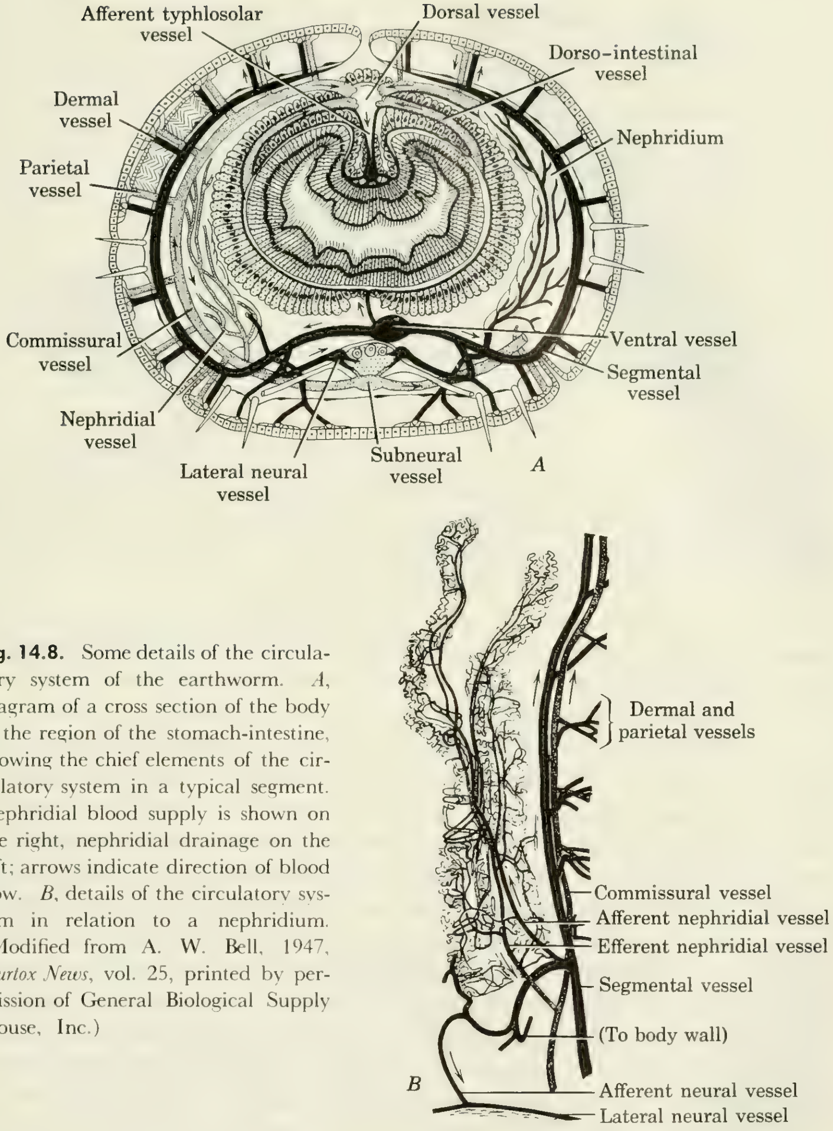

Afferent typhlosolar vessel
Dorsal vessel
Dorso-intestinal vessel
Dermal vessel
Nephridium
Parietal vessel
Commissural vessel
Ventral vessel
Segmental vessel
Nephridial vessel
Lateral neural vessel
Subneural vessel
A
Dermal and parietal vessels
Commissural vessel
Afferent nephridial vessel
Efferent nephridial vessel
Segmental vessel
(To body wall)
B
Afferent neural vessel
Lateral neural vessel

Fig. 14.8. Some details of the circulatory system of the earthworm. *A*, diagram of a cross section of the body in the region of the stomach-intestine, showing the chief elements of the circulatory system in a typical segment. Nephridial blood supply is shown on the right, nephridial drainage on the left; arrows indicate direction of blood flow. *B*, details of the circulatory system in relation to a nephridium. (Modified from A. W. Bell, 1947, *Turtox News*, vol. 25, printed by permission of General Biological Supply House, Inc.)

metabolic wastes. Special additional functions occur in specific organs: in the capillary beds of the body wall, for example, oxygen diffusing through the skin is taken up by the blood, and carbon dioxide is lost to the surrounding air. In the wall of the stomach-intestine the blood receives the absorbed products of digestion. In the nephridia, although the functional details of these organs are not completely understood, the capillary blood flow apparently carries back into the general circulation salts reabsorbed by the cells of the nephridial tubules; we shall return to this point shortly. The complexity and efficient

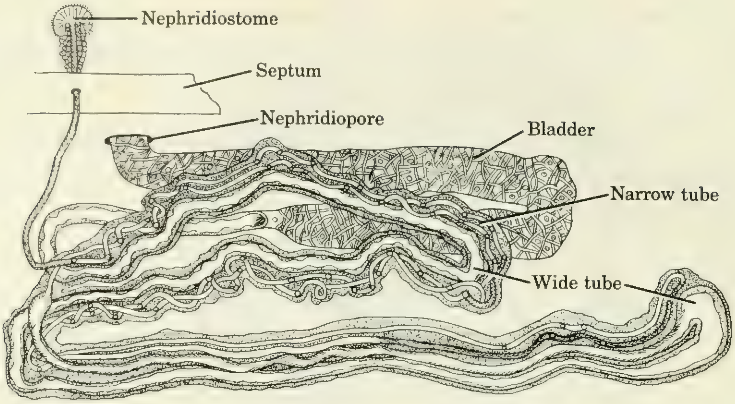


Fig. 14.9. Nephridium of *Lumbricus*, as seen in optical section; somewhat diagrammatic. By following the convolutions of the tubule from the nephridiostome to the exit through the body wall, local differentiations in the characteristics of its walls become obvious. These differences are apparently related to specific differences in function. The extensive capillary networks which cover the nephridium have been removed (cf. Fig. 14.8). (Redrawn from W. B. Benham, 1891, *Quarterly Journal of Microscopical Science*, vol. 32.)

organization of the circulatory system in *Lumbricus* will be apparent from Figure 14.8.

The **excretory system** is comparable with that of *Nereis*, although in *Lumbricus* the individual nephridia are larger and appear to be more highly specialized (Fig. 14.9). Each is a coiled tubule, bearing at its inner end, exposed to the coelomic fluid, a ciliated funnel, the **nephridiostome.** The nephridiostome lies in the coelomic cavity of the somite just anterior to that in which the tubular portion is found; the tubule passes through the intervening septum before becoming thrown into loops. The distal portion is expanded into a bladder-like swelling, lying near the point at which the tubule pierces the body wall to terminate externally in a **nephridiopore.** Parts of the tubule, in addition to the nephridiostome, are ciliated; the loops of the tubule are interlaced with capillaries, and the entire mass is enclosed by peritoneum. The morphological relationships are such that two functional interpretations are possible: (1) the open coelomic funnels may be unimportant in the excretory process, the tubular portions extracting wastes rather from the blood flowing through the nephridial capillary networks; or (2) coelomic fluid may pass into the nephridiostomes and be conducted through the tubules, undergoing modification by the activities of cells lining the tubules—these cells extract from the fluid certain salts which then pass into the circulating blood in the nephridial capillaries. At present, studies in the structure and function of the nephridia of *Lumbricus* favor the second of these interpretations. The urine which may be collected from the bladder region of the nephridium is more watery than that collected in the upper portions of the tubule, indicating that salts have been withdrawn from the urine during its passage through the convoluted, glandular portions of the nephridium. On the basis of earlier research it has been assumed that metabolic wastes may be accumulated and stored as granular deposits in the **chloragogue cells**, modified peritoneal cells covering the digestive tract and particularly concentrated about the dorsal and dorsointestinal blood vessels. The assumption has been that upon the disintegration of these cells their granules were released into the coelomic fluid, whence they were removed by the nephridia. More recent investigations, involving isolation and analysis of the intracellular granules, have established the fact that they do not contain nitrogenous wastes but may represent stored protein reserves. The role of the chloragogue cells in excretion thus appears to be questionable.

Relatively little is known of the specific metabolic processes of the earthworm and similar annelids. Analysis of what is known and comparison of the facts with the well-known functions of higher animals, however, indicate that the processes are entirely comparable.

Structures and Function Related to Responsiveness. The nervous system, with its **cerebral ganglia, circumpharyngeal commissures, ventral nerve cord, subepidermal plexus,** and **nerves,** is essentially like that of *Nereis*. The notable difference in the sensory-neural system appears in the anterior region. *Nereis* is an active, predatory animal, whereas the earthworm is less active and does not seek or capture prey in feeding. In correlation with these different ways of life, *Nereis* is well equipped with sense organs and has a well-differentiated head region; the earthworm has nothing that can properly be called a head and lacks tentacles, palps, and eyes, although the anterior end of the body is the region most sensitive to stimulation.

Earthworms react to mechanical stimuli, withdrawing or extending the body on contact with foreign objects, or retreating into their burrows in response to vibrations transmitted through the ground. Evidences of response to chemical stimuli appear in their reactions to food, which is to some extent selected as though by a sense of taste. Earthworms also detect food a short distance away, as though by some form of olfaction. Sensitivity to light is revealed by the nocturnal habits of earthworms, as well as by their withdrawal reactions when light is flashed upon the surface of the body. Sense organs have long been recognized in the surface layers of the body wall, although only comparatively recently has much progress been made in identifying the specific receptors involved in reactions to different kinds of stimuli. Sense organs which resemble taste buds are present, as well as specialized cells which appear to function in the perception of light.

The cellular basis of the reaction to stimuli is shown diagrammatically in Figure 14.10. Receptor cells in the epidermis respond to specific stimuli by conducting impulses into the subepidermal nerve plexus, and along nerve fibers which pass into the ventral nerve cord. Within the cord these **afferent fibers** make synaptic connections with **adjustor** or **association neurons.** The adjustors, in turn, conduct impulses to other association neurons which distribute the excitation to other regions of the central nervous system. From

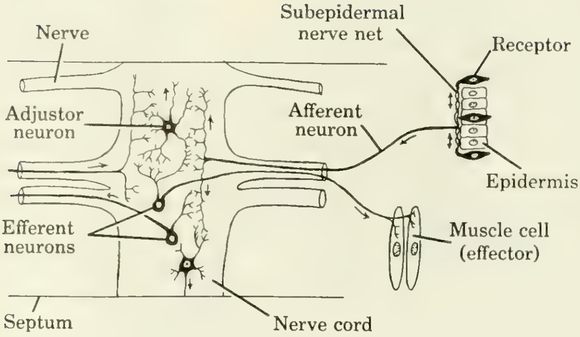


Fig. 14.10. Diagram of the sensory-neuro-muscular mechanism of the earthworm. Arrows indicate direction of conduction of nerve impulses.

the adjustors impulses are also conducted to appropriate **efferent neurons** whose fibers conduct the impulses out of the nerve cord to muscular or glandular cells, the **effector organs.** Alternatively, the pathway may omit the adjustor neurons and pass directly from the afferent fiber to an efferent neuron, the conduction occurring within the ventral nerve cord. A comparison between this system and the reflex mechanism in the nervous system of vertebrates (p. 96) shows that the relationships between cells are essentially the same in the two systems. The receptor cells of the annelid may be compared with such receptors as the olfactory cells of vertebrates, which are similarly located in the epidermis and send nerve fibers into the central nervous system (pp. 109–110). The relationships of the dorsal root cells (afferent neurons) in the vertebrate are more complex, but the differences involve chiefly the interpolation of an additional neuron between the receptor cell and the adjustor neuron. The adjustor and efferent neurons have identical relationships in the annelid and the vertebrate, although in correlation with the greater structural complexity of the vertebrate the adjustor or association mechanism is more elaborate.

The Reproductive System, Reproduction, and Development. Unlike *Nereis*, earthworms are monoecious, and the **reproductive systems** are permanently developed, involving a complex group of accessory structures (Fig. 14.11). There are two **ovaries,** attached to the posterior face of the septum, near the ventral body wall, in somite 13. The **oviducts** are short tubes with expanded funnel-like openings, located just posterior to the ovaries. These funnels receive the ova emerging from the ovaries and conduct them into a small **ovisac,** an expanded chamber in each oviduct. Here the eggs may be retained for some time before they are "laid." Like nephridia, the oviducts pass through a septum before piercing the body wall to reach their external openings. The **testes** are four in number and are located in segments 10 and 11, being attached to the posterior surfaces of septa, as the ovaries are. In the adult worm the testes are enclosed within a cavity formed by the fusion and growth of three pairs of **seminal vesicles,** which partition off a part of the coelom. Within the spacious chamber thus formed the male gametes, detached from the testes in an immature state, complete their maturation.

The male efferent ducts begin within the seminal vesicles as two pairs of fluted funnels, one funnel lying posterior to each testis. From each funnel, a **ductus efferens** (vas efferens) passes through the wall of the vesicle; the two ductus efferentes on each side unite in the coelom to form a **ductus deferens**, which passes through the body wall in segment 15 and opens externally in a male genital pore. The final items in this complex reproductive system are two pairs of **seminal receptacles**. These are sac-like structures protruding into the coelom in segments 9 and 10, opening only on the outer surface of the worm. Their function is to receive spermatozoa from another individual during copulation and to retain these spermatozoa until the subsequent time of fertilization of the eggs. The system is so arranged that only spermatozoa from the seminal receptacles can fertilize the eggs of the individual to which the receptacles belong, thus insuring cross-fertilization.

During **copulation**, spermatozoa accumulated in the seminal vesicles of each worm are transferred to the seminal receptacles of its partner, passing by way of the external seminal grooves (Fig. 14.12). These sperm pathways are protected by their positions during the temporary union and by mucous sheets with which the two worms cover these regions of their bodies at the time of mating. The female portions of the system do not function until later, when eggs are emitted to the exterior and fertilization occurs. At such times a girdle-like cocoon is secreted by the glandular cells of the clitellum and then moved anteriorly by peristaltic contractions of the body. As this cocoon passes segment 14, ova are deposited within it from the openings of the oviducts. As it passes the openings of the seminal receptacles, farther anteriorly, spermatozoa received during copulation are likewise discharged into the space between the girdle and the body wall, and fertilization occurs. Finally,

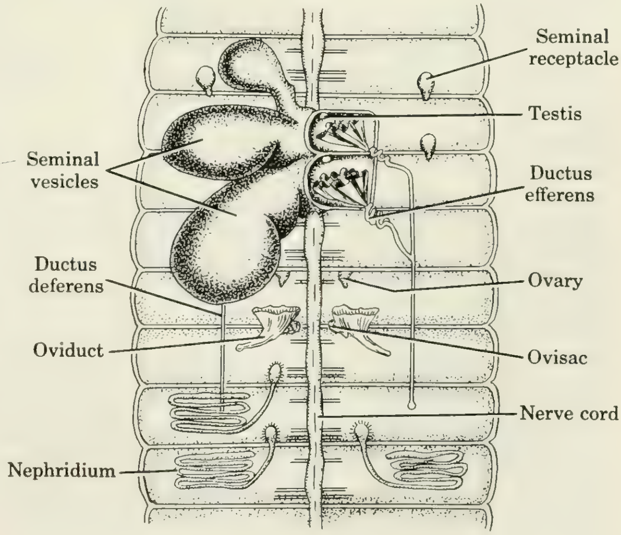


Fig. 14.11. Dorsal view of the reproductive system of the earthworm; semidiagrammatic. The cavities of the seminal vesicles have been exposed on the right side, revealing the testes and the funnels of the ductus efferentes.

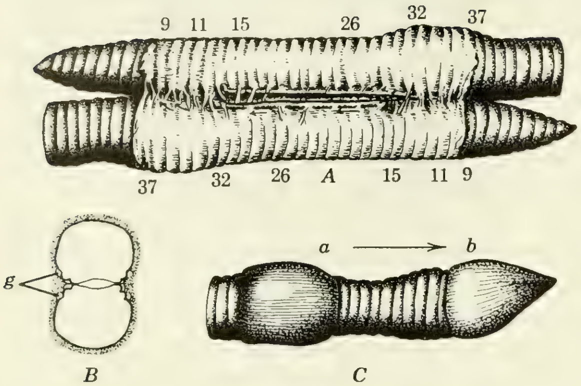


Fig. 14.12. Copulation and cocoon formation in the earthworm. *A*, two worms encased in a sheath of mucus secreted by epidermal glands, as spermatozoa are exchanged along the seminal grooves (arrows). *B*, transverse section, showing mucus sheath and four seminal grooves (*g*), two on each worm. *C*, formation of the cocoon or egg capsule by the clitellar glands of one individual; the cocoon passes anteriorly (*a* to *b*) until it is slipped off as the completed capsule, containing several zygotes. Certain of the somites are numbered for orientation.

the girdle is slipped off over the anterior end of the worm; its ends close, and it becomes an egg capsule, containing a nutrient fluid and several zygotes which develop into miniature earthworms before emerging. The course of embryonic development (Fig. 14.13) is much modified as compared with that of *Nereis* and other polychaetes; there is, of course, no stage corresponding to the free-swimming trochophore of the marine forms. In its main features, such as type of cleavage, mode of origin of mesoderm and coelom, and development of segmentation, however, the embryogeny of the highly specialized earthworm falls in line with that of the more generalized annelids.

Regeneration. Earthworms have a considerable ability to replace whole somites or entire groups of somites by a process of regeneration of lost parts. It is not surprising, considering the greater specialization of the anterior end, and the fact that in ordinary growth somites are regularly added at the posterior end, to find the capacity of regeneration more restricted anteriorly than posteriorly. For example, when pieces are cut from the posterior end of the "manure worm," *Allolobophora foetida*, the animal forms a few new somites and then others, by addition, just as somites are normally added posteriorly during growth. When somites are removed at the anterior end, however, a maximum of only five can be regenerated. A new head may be formed, but the individual never restores the full number if more than five have been removed. When the region containing the reproductive organs is removed, it is not regenerated. In *Tubifex tubifex*, a common, small, fresh-water oligochaete, regeneration is extensive and rapid; an average of 31 new somites may be formed in 32 days. This regeneration has been shown to occur largely through the activities of **totipotent cells**, or **neoblasts**, which migrate to the region of injury and differentiate during regeneration (see the discussion of regeneration in planarians, p. 322). *Tubifex* can regenerate only three or four somites at its anterior end, and neoblasts apparently do not migrate into the anterior regenerating region from other parts of the body. The importance of neoblasts in the regeneration of *Tubifex* has been confirmed by experiments in which injured worms were exposed to X-radiation. When the worms are given a suitable treatment with such radiation, the neoblasts are selectively

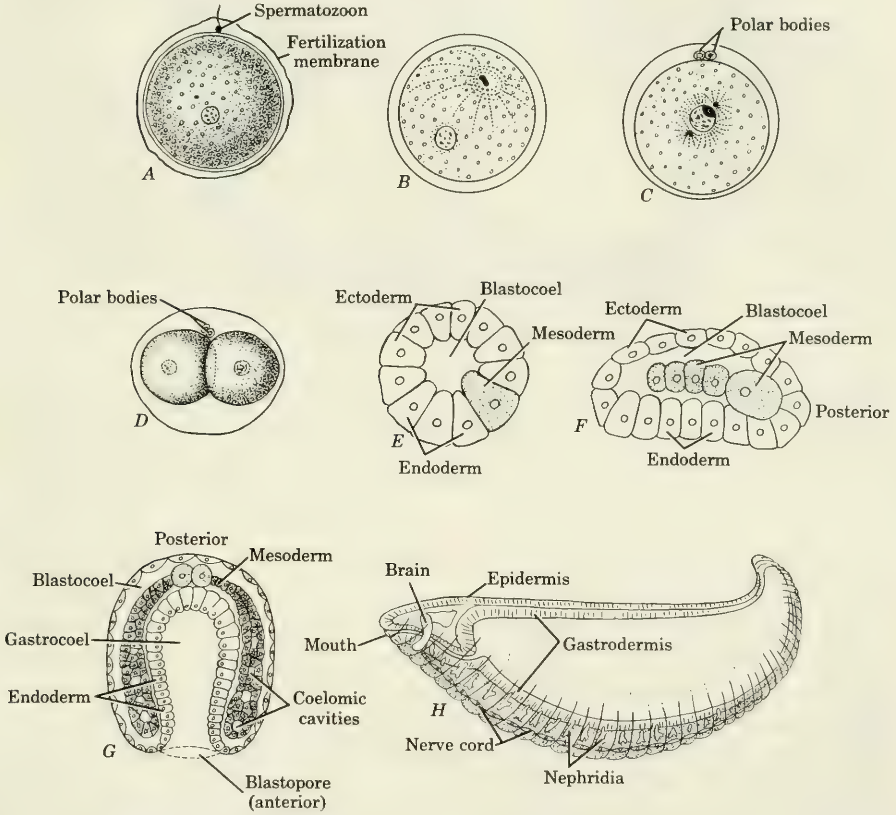

Spermatozoon
Fertilization membrane
A
B
Polar bodies
C
Polar bodies
D
Ectoderm
Blastocoel
Mesoderm
E
Endoderm
Ectoderm
Blastocoel
Mesoderm
Posterior
F
Endoderm
Posterior
Mesoderm
Blastocoel
Gastrocoel
Endoderm
Coelomic cavities
G
Blastopore (anterior)
Brain
Epidermis
Mouth
Gastrodermis
H
Nerve cord
Nephridia

Fig. 14.13. Development of the earthworm. *A* and *B*, penetration of the ovum by a spermatozoon and activation of the maturation process in the ovum. *C*, fusion of male and female pronuclei; note the extruded polar bodies. *D*, two-cell cleavage stage. *E*, section of an early blastula, showing the blastocoel and the cells that will give rise to ectoderm, endoderm, and mesoderm in later development. *F*, parasagittal section of a late blastula, showing particularly the proliferation of mesodermal cells from the mesoblast into the blastocoel. *G*, frontal section of an embryo (late gastrula); note the relationship of the developing coelomic cavities to the old blastocoel, in the typical schizocoelous method of coelom formation. *H*, late embryo, in which the basic organization of the organ systems of the future adult is recognizable; the epidermis and parts of the nervous system have arisen from ectoderm, the gastrodermis has arisen from endodermal cells, and structures between gastrodermis and epidermis are generally of mesodermal origin. (Based on figures and descriptions by E. B. Wilson, 1889, *Journal of Morphology*, vol. 3.)

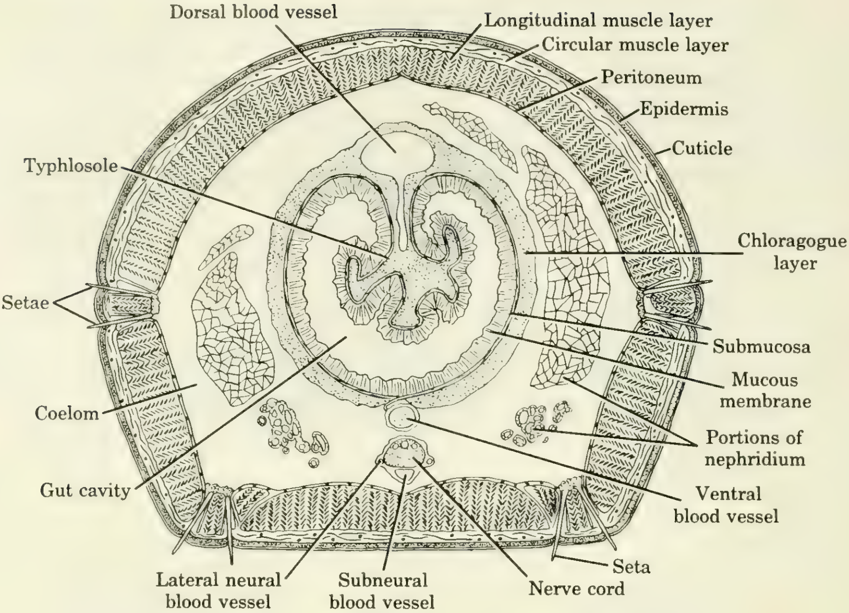

Dorsal blood vessel
Longitudinal muscle layer
Circular muscle layer
Peritoneum
Epidermis
Cuticle
Typhlosole
Chloragogue layer
Setae
Submucosa
Mucous membrane
Coelom
Portions of nephridium
Gut cavity
Ventral blood vessel
Seta
Lateral neural blood vessel
Subneural blood vessel
Nerve cord

Fig. 14.14. Diagrammatic cross section of the earthworm, through the region of the stomach-intestine. As shown here, such a section contains only irregular portions of septa and nephridia.

destroyed, apparently without injury to other cells. The individuals thus treated are unable to regenerate.

Cellular Structure and Functions. The cellular structure of the earthworm includes tissues of all the principal classes **epithelial, sustentative, vascular, contractile,** and **nervous**—although within these classes there is less extreme specialization than in the corresponding tissues of vertebrates. As shown by a transverse section of the body in the region of the stomach intestine (Fig. 14.14), the body wall is covered externally by a delicate, non-cellular **cuticle,** perforated where gland cells and sensory cells are exposed at their outer ends. The cuticle is secreted by the underlying **epidermis,** a single layer consisting of **columnar epithelial cells.** Scattered among the epithelial cells are numerous **receptor cells** and the **gland cells** that secrete the fluid found upon the surface of the body. Beneath the thin basement membrane upon which the epidermis rests is a **circular muscle layer** composed of non-striated fibers lying in a plane parallel to that of the transverse section. Contraction of these muscles decreases the diameter of the body, compresses the coelomic fluid, and results in an increase in the length of the body. Within this outer muscular layer there is a considerable amount of **fibrous connective tissue; vascular tissue** is also abundant here, for this layer of the body wall is the site of gas exchange between the blood and the external environment. Beneath the circular muscle layer is a layer of **longitudinal muscle fibers;** these fibers extend in planes perpendicular to that of the transverse section. In such a section the inner muscular layer has a feathery appearance, because its fibers are arranged along the surfaces of sheets of connective tissue, to which they are attached. Contraction of the longitudinal muscles is antagonistic to the action of the circular muscles; they shorten the body, compressing the coelomic fluid and resulting in an increase in the diameter of the worm. Coordinated, localized contraction and relaxation of these two muscle layers are responsible for the peristaltic locomotor movements of the worm, operating in conjunction with changes in the positions of the setae. The layer of longitudinal muscle fibers is bounded internally by the **parietal peritoneum,** the lining of the coelomic cavities, consisting of a **squamous epithelium** of mesodermal origin.

The internal surface of the body wall, the anterior and posterior faces of the septa, and all other parts structurally related to the coelom are covered by the continuous peritoneal epithelium. The layer covering the outside of the digestive tube is spoken of as the **visceral peritoneum,** as in vertebrates. In the earthworm and related annelids, this layer is modified from the usual squamous type to form a columnar epithelium, composed of the chloragogue cells referred to on page 409 in connection with excretion. Beneath this layer the gut wall consists of the following components: a thin **submucosa,** made up of connective tissue; a layer of non-striated muscle fibers, both circular and longitudinal in orientation; and a single-layered epithelium

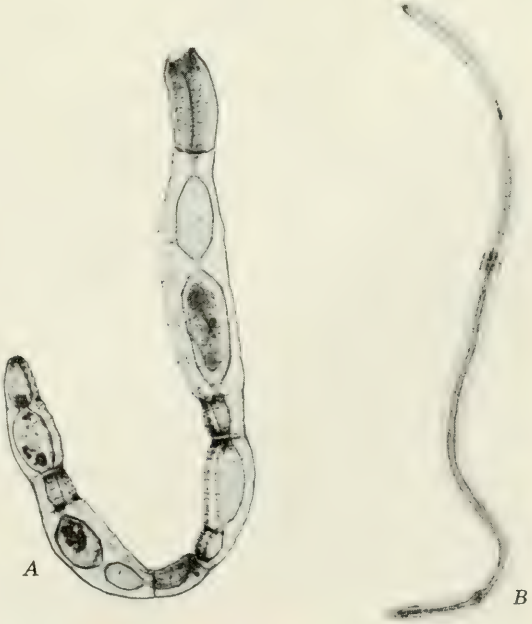


Fig. 14.15. Asexual reproduction in aquatic oligochaetes. *A*, *Chaetogaster diaphanus; B*, *Tubifex tubifex.* (Photographs by Bassett Maguire, Jr.)

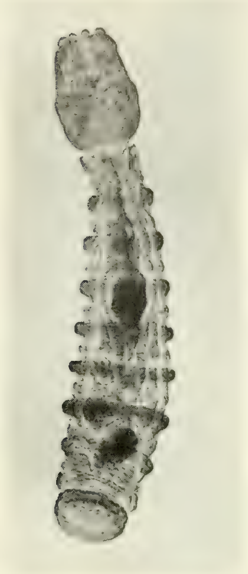


Fig. 14.16. A branchiobdellid worm, *Cambarincola philadelphica.* This small oligochaete, with superficial resemblances to a leech, clings to its host, the crayfish, by means of the expanded posterior sucker. (Photograph courtesy General Biological Supply House, Inc.)

lining the digestive cavity. The submucosa and the muscular layer contain numerous capillaries important in the absorption of products of digestion. The digestive epithelium is composed of **columnar cells** and **gland cells.** As in other metazoans, this is the layer from which digestive enzymes are secreted into the lumen and through which absorption occurs. The extensive, dorsal typhlosole of the stomach-intestine is analogous to the numerous villi and rugae of the vertebrate intestine; all function to increase the secretory and absorptive area of the wall of the gut.

Other Oligochaetes. There are well over 1800 species of earthworms and hundreds of additional species of aquatic oligochaetes. With this in mind, and considering also the diverse conditions of existence to which these various forms have become adapted, we should not expect all oligochaetes to resemble *Lumbricus* in detail. Nevertheless, *Lumbricus* is fairly typical of the general annelid grade of organization. Other oligochaetes, ranging in size from tropical earthworms which may reach 6 or 8 feet in length to fresh-water worms measuring less than a millimeter, present many interesting structural and functional modifications. *Tubifex* (Fig. 14.15), for example, a small aquatic form, customarily lives with its anterior end buried in mud. The posterior portion is extended and waves about in the water, seeking a level containing adequate amounts of dissolved oxygen. In *Tubifex* gas exchange occurs chiefly through the wall of the intestine, cutaneous gas exchange being subsidiary. In these and many other small oligochaetes, the capillary beds characteristically present in the intestinal submucosa of *Lumbricus* are represented by large, continuous blood sinuses, although the remainder of the vascular system is "closed." Reproductive habits vary; in many small aquatic forms sexually mature individuals have never been recognized, and reproduction occurs exclusively by a process of transverse fission (cf. rhabdocoel turbellarians, p. 325). One entire family of aquatic oligochaetes, the Branchiobdellidae (Fig. 14.16), have become adapted to an ectocommensal or ectoparasitic existence. These minute worms pass their complete life cycles attached among the gills and swimmerets of the freshwater crayfish. In correlation with this way of life, they show several modifications, notably an expanded posterior sucker for adhesion to the host.

The Class Archiannelida

The Archiannelida are small marine worms which as adults resemble in many ways the juvenile stages of polychaetes. As previously indicated, the archiannelids may be considered as either primarily simple, generalized forms or as secondarily simplified types. The varying characteristics of members of this class indicate that they may not constitute a taxonomically homogeneous group. A representative example, *Polygordius*, shows externally only indistinct evidences of segmentation (Fig. 14.17). Internally, however, it possesses the metamerism and other features characteristic of the phylum. The developmental sequence of stages in *Polygordius*, involving a typical trochophore larva with gradual metamorphosis into an elongate, segmented adult, is so simple and straightforward that it has been extensively studied as typical of the primitive development of annelids.

The Class Hirudinea

The Hirudinea, or leeches, are predominantly fresh-water annelids, although some are marine and others have become adapted to life in a moist terrestrial environment. Most leeches are temporarily or permanently ectoparasitic, feeding on the blood of vertebrate hosts. Some fresh-water species are known which are not parasitic but feed instead on snails and other small aquatic organisms. The typical annelid structure is the fundamental plan of organization in leeches, although in correlation with the parasitic habit of the group considerable modification and specialization have occurred (Fig. 14.18). The body has 32 segments, each subdivided externally into three or more rings, and is conspicuously flattened dorsoventrally. There are no parapodia and no setae. Some leeches have horny jaws with which incisions are made in the skin of the host; others have an unarmed proboscis. The mouth lies in the center of a small oral sucker, used in feeding and in locomotion; a larger sucker at the posterior end holds the leech securely upon its host or elsewhere. In locomotion looping movements are executed, the

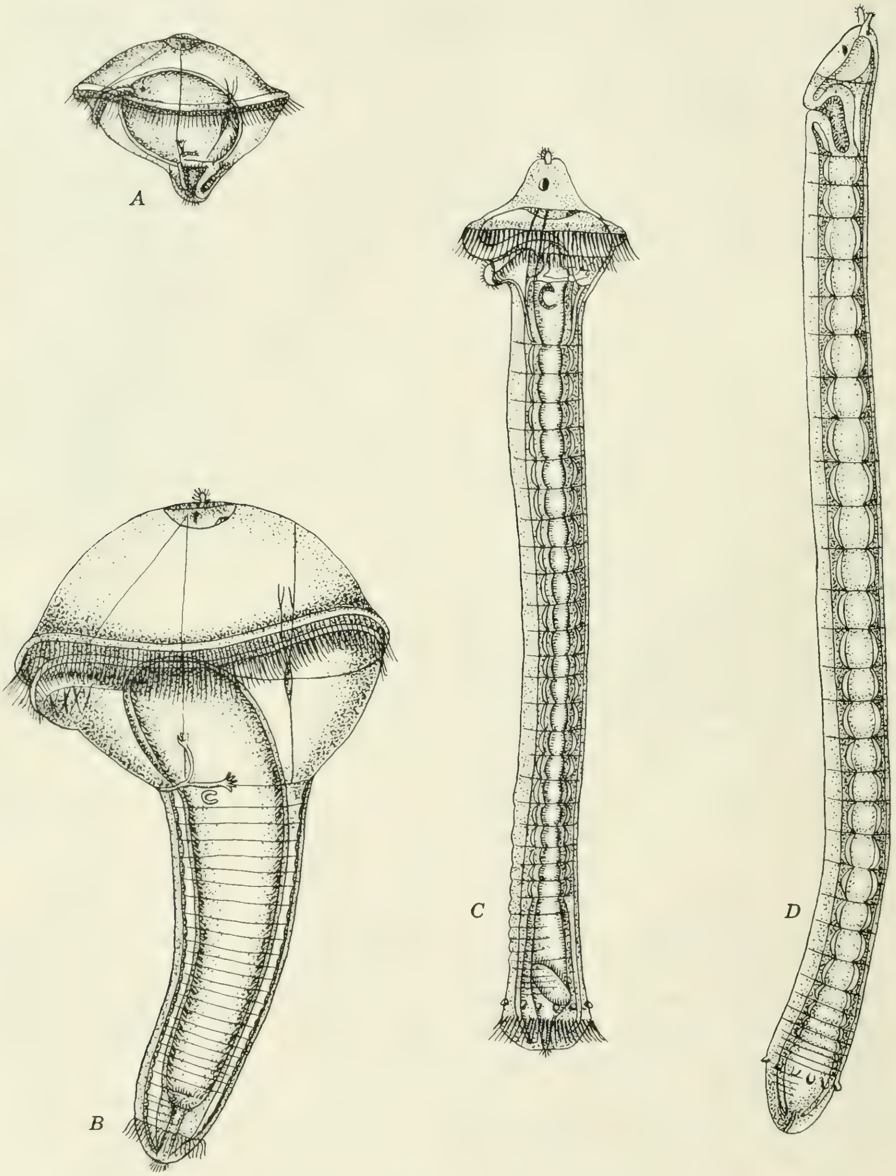


Fig. 14.17. Class Archiannelida: development of *Polygordius*. *A*, trochophore larva. *B*, early stage in the development of the segmented, wormlike body. *C*, intermediate stage. *D*, young adult worm. Note the presence, in the early stages, of a protonephridial system which disappears during the transformation to adulthood. The zone of growth lies just anterior to the last segment. (Redrawn from B. Hatschek, *Studien über Entwicklungsgeschichte der Anneliden*, Vienna, 1878.)

two suckers being alternately attached and released. When unattached, the animal may swim by sinuous, undulatory movements.

Internally, the leech presents many modifications of the annelid structural organization (Fig. 14.19). The **digestive tract** bears many pouch-like **caeca** for the prolonged storage of ingested blood; the animal may go for long periods without feeding. The coelom is much reduced, the cavity being restricted to channels within a spongy meshwork of mesenchymatous tissue.

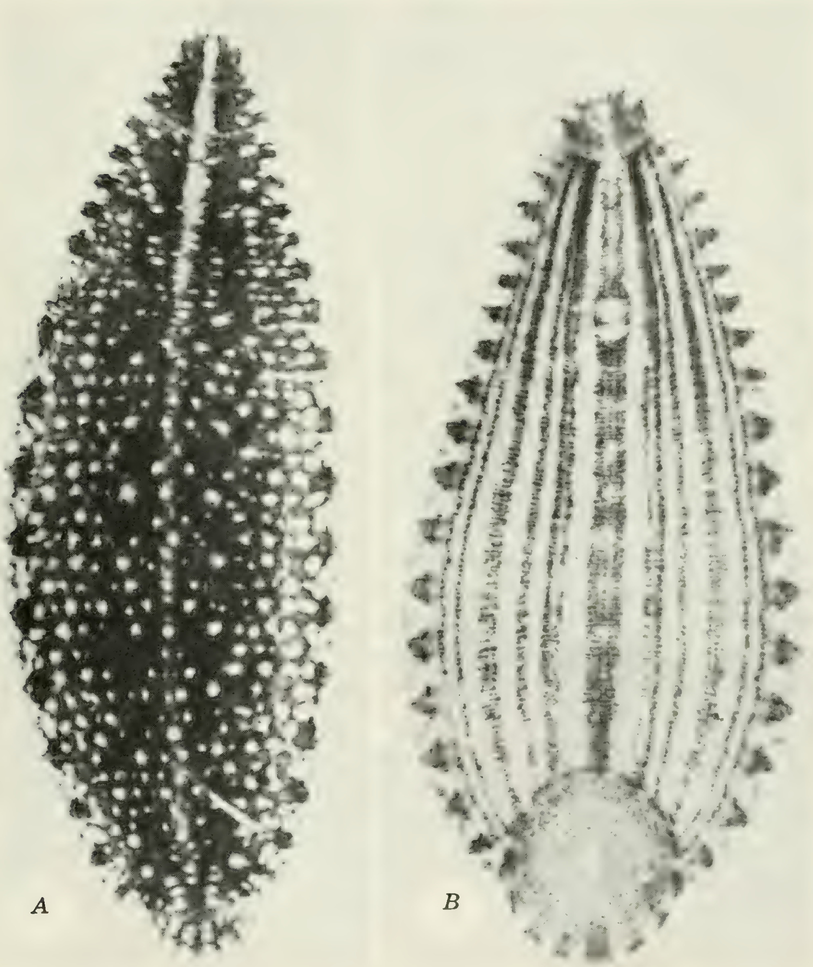


Fig. 14.18. Class Hirudinea. A common fresh-water leech, *Placobdella parasitica*. *A*, dorsal aspect; *B*, ventral aspect. Note the anterior and posterior suckers and the division of the body into a large number of apparent segments. (From Master's Thesis of M. H. Woods, 1940, Cornell University.)

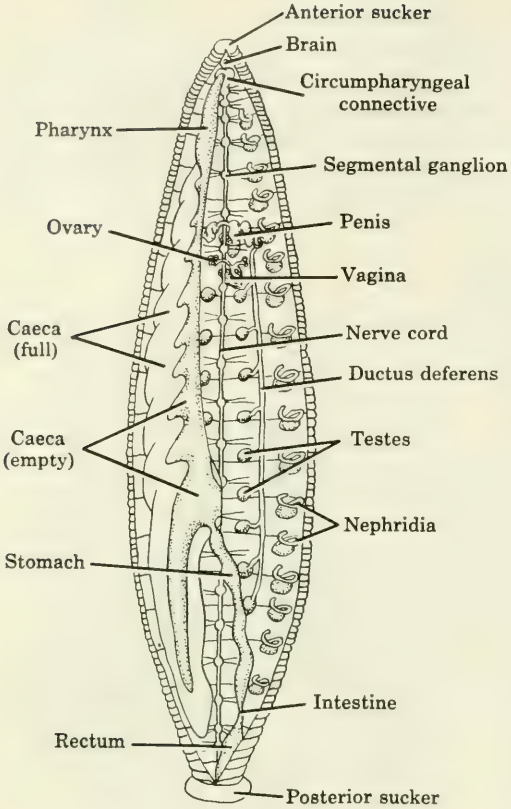

Anterior sucker
Brain
Circumpharyngeal connective
Pharynx
Segmental ganglion
Ovary
Penis
Vagina
Caeca (full)
Nerve cord
Ductus deferens
Caeca (empty)
Testes
Nephridia
Stomach
Intestine
Rectum
Posterior sucker

Fig. 14.19. Class Hirudinea. Dorsal view of the medicinal leech, *Hirudo medicinalis*, showing the general arrangement of internal organs. (Redrawn, after Parker and Haswell, from F. A. Brown, Jr., in F. A. Brown, Jr., *et al.*, *Selected Invertebrate Types*, copyright 1950 by John Wiley and Sons, Inc., printed by permission.)

Larger coelomic spaces persist in connection with the segmental nephridia and within the reproductive organs.

Structurally, and to some extent functionally, the leeches show many evidences of affinities with the oligochaetes. The indications are that the two groups have evolved in different directions from common, or at least similar, ancestry.

Some fresh-water leeches are dangerous parasites of man and domestic animals. Some large leeches have an estimated capacity of 8 milliliters of blood. The terrestrial leeches found in many tropical countries of the Orient are serious pests. They occur on or near the ground, in the dank vegetation of the rain forests, and attach themselves to men and animals passing by.

The Annelid Body Plan

The type of structure found in annelids is important for comparison with the plans of organization of simpler and of more complex metazoans. In such comparative considerations the significant features of annelids involve chiefly

(1) the simple, generalized condition of metamerism and (2) the development and relationships of the coelom and its derivatives. In comparison with the acoelomate, non-metameric turbellarians, for example, the annelid plan is considerably advanced. Comparison with a more complex metazoan, such as an arthropod or a vertebrate, shows that the relative complexity of these higher forms is largely a difference in degree. The fundamental characteristics of metamerism and of the coelom are firmly established in the annelid; the more advanced structural features of arthropods and of vertebrates may be interpreted as elaborations and modifications of a basic plan already laid down in the annelids or in their ancestral stock. This is the more interesting when we reflect that both segmentation and the coelom apparently originated differently and evolved independently, in the annelid-arthropod stock and in the echinoderm-chordate line (see Fig. 7.3, p. 219). In any case, in none of the metazoan phyla more advanced than the annelids are the characteristics of metamerism and coelom present in such an uncomplicated condition as in these segmented worms.

Even within the phylum Annelida, evolution has involved departures from the primitive conditions in these characteristics. The process of **cephalization,** the development of anteroposterior differentiation, has progressed to a considerable degree in the higher annelids. Along with cephalization there has been an increase in regional specialization. As a result, the originally uniform series of similar somites has become organized into a series of differentiated groups of somites, each group modified for the performance of some particular function. This has involved general structure, the appendages, and the internal organs as well, and it is perhaps best demonstrated among the sedentary, tube-dwelling polychaetes. The oligochaetes and leeches furnish examples of variant modifications of the originally undifferentiated and extensive coelomic pouches. In specifically delimited regions of the body these have been given over to reproductive functions; in the Hirudinea they have all but disappeared.

Other annelid characteristics should be emphasized in anticipation of our discussions, in the next chapter, of the phylum Arthropoda. Throughout their history, the annelids have retained and developed, as the basic locomotor mechanism, the body-wall musculature, consisting of concentric sheets of antagonistic circular and longitudinal muscle fibers. In correlation with the type of locomotion to which they are thus limited, and with their cutaneous method of respiration, the annelids have retained the thin, flexible, secreted cuticle as a protective cover for the body wall. The nervous system, organized on the basis of quasi-independent segmental units, is also significant. All these characteristics, as we shall see, foreshadow special conditions to be encountered among arthropods.

CHAPTER 15

JOINT-FOOTED ANIMALS AND

The Phyla Arthropoda and Onychophora

The Phylum Arthropoda

Like the Annelida, the Arthropoda are bilateral, triploblastic, segmented animals. Unlike the annelids, however, the arthropods have a much reduced coelom, and the cuticle which covers the body in annelids is represented in arthropods by a hardened exoskeleton which must be periodically shed to permit growth. The name Arthropoda, which means "joint-footed," refers to another conspicuous feature, the fact that the appendages are composed of several divisions, so hinged together as to be capable of specific movements. The taxonomy of arthropods is difficult and necessarily complicated, owing to the relatively large number of different types of animals which possess the general characteristics of the phylum but show important distinctions indicating varying degrees of interrelationship. The scheme we shall follow, although it is not sufficiently detailed to satisfy a specialist, will nevertheless take into account many of these distinctions.

We shall consider the phylum Arthropoda to be composed of three subphyla: the subphylum **Trilobitomorpha**, the subphylum **Chelicerata**, and the subphylum **Mandibulata**. The first of these is a group of extinct arthropods, represented by the Trilobita, which had a long evolutionary history dating from Pre-Cambrian times but are now known only as fossils. The members of the subphylum Chelicerata are set apart from other arthropods because they are without antennae, or specialized sensory outgrowths from the head,

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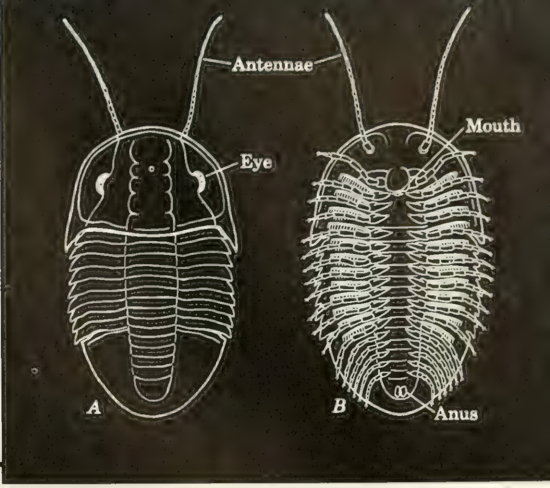

Fig. 15.1. Subphylum Trilobitomorpha. *A*, dorsal view, and *B*, ventral view of a generalized trilobite. The appendages are all relatively unspecialized; the fringed lateral processes are interpreted as epipodites, which probably served for gaseous exchange. (Redrawn from R. E. Snodgrass, *Textbook of Arthropod Anatomy*, copyright 1952 by Cornell University Press, printed by permission.)

and the first pair of ventral appendages are modified into pincer-like structures termed **chelicerae.** The Chelicerata include four classes: the class **Xiphosurida,** containing "horseshoe crabs" of the genus *Limulus;* the class **Eurypterida,** an extinct group represented by the "sea scorpions" such as *Eurypterus;* the class **Pycnogonida,** peculiar, long-legged animals known as "sea spiders"; and the class **Arachnida,** which contains the familiar spiders and scorpions.

The subphylum Mandibulata, as the name implies, includes those arthropods in which a pair of appendages flanking the mouth are adapted as **mandibles,** or jaws. Of the several classes grouped in this subphylum, the most important are the class **Crustacea,** mostly aquatic forms such as the lobster, the crayfish, and the crabs; the class **Chilopoda,** or centipedes, with long, many-segmented bodies and reproductive ducts which open posteriorly; the class **Diplopoda,** in which the segments are fused in pairs and the openings of the reproductive ducts are anterior; and the class **Insecta,** which are mostly terrestrial, wing-bearing arthropods with three pairs of walking legs. Familiar insects include flies, beetles, and butterflies.

The habitats of arthropods are more diverse than those of any other phylum. Arthropods are found abundantly in the ocean, in fresh water, and on land, and most of the insects are adapted for flight. In correlation with this diversity of habitat the species present a great variety of habits and structural modifications, although the arthropod type of organization is well defined by segmentation, the exoskeleton, and the jointed appendages. No other phylum of animals approaches the arthropods in numbers of species. It has been estimated that the number of species of insects alone is well over 1,000,000, as compared with a total of some 37,500 species of chordates and 60,000 species of mollusks. If we add to the insects an estimated 30,000 species of crustaceans, 16,000 species of chelicerates, and 2000 species of chilopods and diplopods, the total is much larger than that of all other species of animals. We are accustomed to think of vertebrates as the dominant forms of terrestrial life at the present day; the vertebrates are far exceeded in numbers of species and numbers of individuals by the insects, which are so numerous that they literally contend with the vertebrates for possession of the earth.

The arthropods are of considerable economic importance. Crustacea, such as lobsters, crabs, and shrimps, are a significant source of food. Certain insects produce silk, others prepare honey, and through the agency of insects many plants useful to man are pollinated. Some insects are beneficial to man in that they prey upon, or parasitize, other kinds of insects. On the other hand, the arthropods include species that destroy almost every form of vegetation, others that are parasitic on man and his domestic animals, and still others that transmit the organisms of disease to man.

The oldest known fossil remains of arthropods are those of trilobites (Fig. 15.1); according to the fossil record, these forms were already abundant and highly specialized in Cambrian times. It is logical to assume that these complex forms arose through a long Pre-Cambrian evolutionary history, and hence that more primitive and generalized arthropod types must have been in existence, possibly for some millions of years, before the beginning of our fossil record. All the modern arthropod groups had arisen and become well diversified by the early part of the Mesozoic Era, roughly 200,000,000 years ago (see Fig. 20.1, p. 617). By this time trilobites had become extinct.

Although Chelicerata undoubtedly arose earlier than Mandibulata, the two most successful and significant modern groups of arthropods are the mandibulate forms included in the classes Crustacea and Insecta. In the discussion to follow, we shall devote our attention chiefly to these two classes, referring more briefly to other arthropods.

THE CLASS CRUSTACEA

The Crustacea, for the most part aquatic animals, include the principal marine representatives of the phylum Arthropoda. During their evolution the crustaceans appear to have spread from their primitive habitat, the ocean, to fresh water and in a few cases to terrestrial life, in a manner reminiscent of the gastropod mollusks. The two principal types of crustaceans, **Entomostraca** and **Malacostraca**, will be considered after we have examined the crayfish as a typical crustacean.

The Crayfish: ***Habitat and Activities.*** Crayfishes are abundant in streams and fresh-water ponds of all the continents and many of the larger

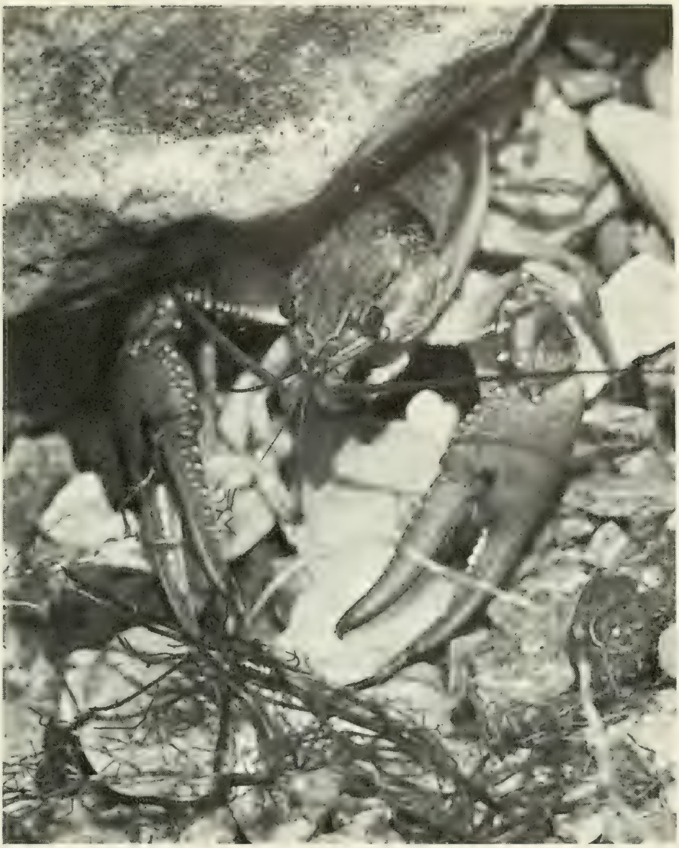

Fig. 15.2. A fresh-water crayfish in its natural habitat, partially concealed under a stone. Note the evident utility to the animal of the elongate, sensitive antennae and antennules and of the movable compound eyes. (Photograph by Charles W. Schwartz.)

islands, such as Tasmania, New Zealand, and Madagascar. Their distribution is limited by certain environmental factors, notably the availability of calcium carbonate in the water. Different species are adapted to various habitats: some frequent rapidly flowing streams; others are found only in stagnant ponds or sluggish streams; still others occur in wet meadows and marshes. Species of the genera *Cambarus* and *Orconectes* are widely distributed in the more temperate regions of North America east of the Rocky Mountains, and several species of the genus *Astacus* are found in the streams of the Pacific Slope. The account of the crayfish that follows is applicable to the common species of *Cambarus* and related forms.

In nature, the crayfish is found crawling upon the bottom or concealed under stones (Fig. 15.2), or in burrows which many species excavate into the banks of ponds and streams. Some forms burrow for considerable distances into the banks, or into the soil of wet meadows far from open bodies of water. They construct entrances and air holes that appear as chimney-like masses of mud brought up and deposited around the openings. The burrow usually terminates in a chamber below or near the waterline.

In moving about upon the bottom of a stream or pond, the crayfish walks slowly forward with its great claws held in front of the body. Its common escape reaction is to dart backward through the water with great rapidity, propelled by sudden strokes of the tail fin. As the animal glides after each stroke, the abdomen is folded under; coming to rest upon the bottom, the animal lifts and expands the abdomen in preparation for another stroke. Crayfishes respond quickly to visual stimuli; but in burrows, where little light penetrates, and in their nocturnal activities generally, various receptor organs for tactile and chemical stimuli must be more significant. Such receptors are generally distributed over the body but are most numerous on the two pairs of antennae. In feeding, the crayfish captures animals, such as aquatic insects and fishes, by lying in wait and seizing them with its claws. It also lives as a scavenger, feeding upon the bodies of animals found dead upon the bottom.

Crayfishes are primarily aquatic animals, but in the laboratory they thrive best if kept where they can crawl out of the water, and they will often remain exposed in a moist atmosphere for hours. In their natural habitats, along a stream at night, crayfishes are sometimes seen upon the bank near the water; they occasionally make nocturnal expeditions of some length upon land, possibly in search of food.

General Structure. As in all segmented animals, the body of the crayfish is composed of a series of somites. These are not all similar, however, but are grouped together and modified to form definite, specialized regions of the body. Three regions, the **head**, the **thorax**, and the **abdomen**, may be distinguished externally. The head and the thorax are fused to form the so-called **cephalothorax**, covered dorsally and laterally by a non-segmented portion of the exoskeleton, the **carapace**. The carapace terminates anteriorly in a pointed **rostrum**, and the boundary between head and thorax is marked on the carapace by a transverse **cervical groove**. In these anterior regions the underlying segmentation of the body, obscured dorsally by the carapace, is revealed ventrally by the segmental origin of a series of paired appendages. In the abdomen the somites are clearly demarked both dorsally and ventrally.

The paired **eyes** and two pairs of sensory appendages, **antennules** and **antennae**, project laterally and anteriorly from their attachments beneath the rostrum. The appendages about the mouth, which are modified to assist in the capture and manipulation of food, are distinguished as oral appendages, or "mouth parts" (Fig. 15.3). Of these, the **mandibles** and two pairs of **maxillae** originate from segments of the head; the following three pairs of oral appendages, the **maxillipeds**, originate from the three anteriormost segments of the thorax. Behind the third maxillipeds arise the great pincer-bearing appendages, the **chelipeds**, which constitute the first of five pairs of walking

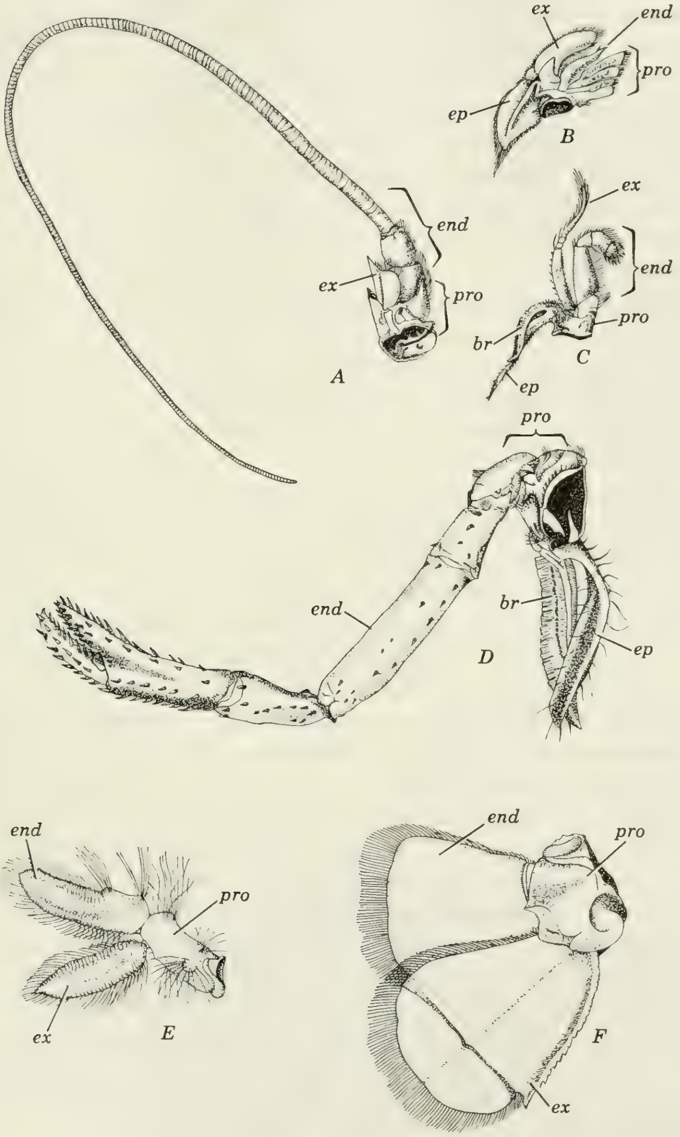
ex
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Fig. 15.3. Comparative aspects of selected appendages of the lobster, *Homarus americanus*. *A*, antenna; *B*, second maxilla; *C*, second maxilliped; *D*, third pereiopod or walking leg; *E*, third pleopod or swimmeret; *F*, uropod. Abbreviations: *ex*, exopodite; *end*, endopodite; *pro*, protopodite; *ep*, epipodite; *br*, branchia. (Redrawn from F. H. Herrick, 1909, *Bulletin of the U.S. Bureau of Fisheries*, vol. 29.)

legs, or **pereiopods**; all these are thoracic appendages. The abdomen bears five pairs of delicate, paddle-like appendages, the **swimmerets,** which function in maintaining water circulation, and to which, in the female, the zygotes are attached at the breeding season. In the male the two anterior pairs of abdominal appendages are strongly modified as copulatory organs, whereas in the female the first pair is very small. In both sexes the most posterior appendages, borne laterally upon the last abdominal segment, are the fan-like **uropods.** A median, flap-like outgrowth of the last segment, termed the **telson,** bears the anus upon its ventral face. The telson is not a segment, and as it is neither paired nor jointed, it is not considered an appendage. The uropods and telson together form the broad tail fin used in swimming.

There are thus 19 pairs of appendages; 5 pairs belong to the head, 8 to the thorax, and 6 to the abdomen. If we assume that each somite bears a single pair of appendages, there are 19 somites in the body. This count is confirmed by the appearance, during the course of development, of 19 pairs of ganglia in the central nervous system, although not all these ganglia are distinct in the adult animal.

Comparing the structure of the appendages, we find that all are based on a similar plan, although some are so greatly modified that the homologies are not clearly recognizable until the developmental stages are examined. The simplest appendages are the swimmerets, which in the adult show the fundamental plan of structure: a basal **protopodite** with two segments, bearing at its distal end two branches, a lateral **exopodite** and a medial **endopodite.** In the pereiopods the protopodite bears in the adult only one distal branch, the endopodite, which is divided into five segments. Exopodites are present on these appendages until a late stage of development but are lost before the animal reaches adulthood. In the maxillipeds the three fundamental divisions, protopodite, exopodite, and endopodite, again appear. In the maxillae and mandibles it is necessary to refer to the developmental stages to determine homologies. The mandible, for instance, bears an exopodite during development but in the adult consists of only protopodite and endopodite. The antennae show the three fundamental parts, with the endopodite greatly elongated. The antennules are similarly divided into a basal segment bearing two distal branches, here both elongated, but their homology with the other appendages is uncertain. The part of the head bearing the eyes and the antennules probably had an origin different from that of the somites, and hence these sensory outgrowths of the head may not be homologous with the segmental appendages.

The basic structural similarity of all the true segmental appendages of the crayfish is interpreted as indicating that at some stage in the remote ancestry of these forms, the somites all bore similar, simple, biramous appendages, possibly resembling the swimmerets of the modern crayfish. As regional specialization of the body developed, the appendages underwent differential modification in adaptation to the more efficient performance of specific operations. The mouth parts, for example, are clearly adapted in a variety of ways for grasping and manipulating food; the development of the chelipeds is similar in nature to that of the other pereiopods, but different in the extent to which it has been carried. In the course of these adaptive processes, various parts of the appendages have developed differently; the exopodites are often reduced in size, and some disappear during the growth stages of the individual. The segmental appendages of such crustaceans as the crayfish offer excellent material for the study of **serial homology.** The progressive nature of the modifications, which are often completed only in the adult stage, is indicative of a certain amount of **recapitulation;** that is, each individual in its development more or less repeats, in abbreviated form, the long history of evolution of its ancestry.

The **gills** are located in the thoracic region, lying in **branchial chambers** covered on each side by a lateral flap of the carapace (Fig. 15.4). The gills are a series of lateral outgrowths of the body wall, protected by the extensions of the carapace, much as the gills of a pelecypod mollusk are covered by the mantle flaps and the shell. In most crayfishes two kinds of gills are distinguished, on the basis of their points of origin: **podobranchiae,** arising with the non-branchial epipodites from the basal segments of the thoracic limbs; and **arthrobranchiae,** arising from the joints by which the thoracic limbs are attached to the body. In the lobster and in some crayfishes there are also **pleurobranchiae** arising from the sides of most thoracic segments. Typically, each thoracic segment bears one pair of podobranchiae and two pairs of arthrobranchiae, but modifications of this plan are frequent.

In concluding this general account of the external features of the crayfish, it should be emphasized that the skeleton is a continuous structure, covering the entire external surface of the animal and even forming the lining of the digestive tract at its anterior and posterior ends. Even the most delicate

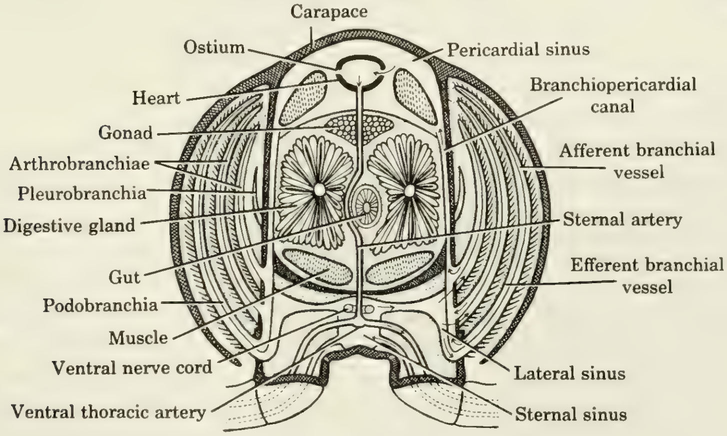

Carapace
Ostium
Pericardial sinus
Heart
Branchiopericardial canal
Gonad
Afferent branchial vessel
Arthrobranchiae
Pleurobranchia
Digestive gland
Sternal artery
Efferent branchial vessel
Gut
Podobranchia
Muscle
Ventral nerve cord
Lateral sinus
Ventral thoracic artery
Sternal sinus

Fig. 15.4. Diagrammatic cross section of a crayfish at the level of the sternal artery (cf. Fig. 15.5). Arrows indicate direction of blood flow.

external parts, such as the feathery gills and the hair-like sensory setae on the appendages, are covered by a thin layer of the skeleton. Like the cuticle of an annelid, the crustacean exoskeleton is a non-cellular, non-living secretion product of the cells of the epidermis. Basically, the exoskeleton is composed of varying proportions of tough **scleroproteins** and a characteristic nitrogen-containing polysaccharide called **chitin.** At points of flexure, as between somites of the abdomen and between divisions of the appendages, the skeleton is thin and flexible. In its thicker portions, as in the carapace, the organic substance of the basic skeleton is hardened by the addition of calcium carbonate. The exoskeleton of the crayfish may be progressively thickened by the deposition of additional material, but it cannot stretch laterally except in the early stages of its formation, before the calcium carbonate has been deposited. As a result of this mechanical relationship between the skeleton and the completely enclosed body, growth cannot occur by continual additions to the skeleton, as it can with the exoskeleton of a mollusk. Hence, the crayfish, like other arthropods, periodically resorbs some of the material of its skeleton and secretes a thin, new skeleton beneath the old one. The old one, including the lining of both ends of the digestive tract, is then shed, or **molted.** In the few hours immediately following such a molt, the crayfish, covered only by the thin, elastic, flexible new skeleton, imbibes water and swells to a larger size. As the new skeleton progressively hardens during the days that follow, the animal assumes again its normal hard-shelled condition. During its soft-shelled state the crayfish is defenseless; and, since its muscles are attached only to the flexible new skeleton, its powers of movement are much impaired. It usually remains in its burrow or otherwise concealed until the skeleton has attained some degree of hardness. The soft-shelled crabs, considered a table delicacy, are merely crabs captured so soon after molting that their shells have not yet hardened.

Structures and Functions Related to Metabolism. The **digestive system** consists of the digestive tract and its appended glandular organs (Fig. 15.5). A short **esophagus** leads from mouth to **stomach,** the anterior portion of which contains the **gastric mill.** This structure has **teeth** or ossicles formed by thickenings of its skeletal lining; the teeth are so arranged that they grind against each other and so complete the mastication of ingested food. Large, paired **digestive glands** open into the anterior region of the **intestine,** immediately behind the stomach. Finely divided particles of food are passed through filters in the stomach and into tubular cavities within the digestive glands. These tubules are lined by an epithelium composed of several types of cells: one type secretes digestive enzymes which accelerate the breakdown of food in the tubules; another type functions in absorption of the products of digestion and in storage of energy reserves such as glycogen and fat. Undigested residues of food are returned into the cavity of the intestine and carried back through the long **hind-gut** for **egestion** at the anus. The intestine apparently serves little or not at all in digestion and absorption; only the portion of the intestine into which the digestive glands open is lined by a mucosa derived

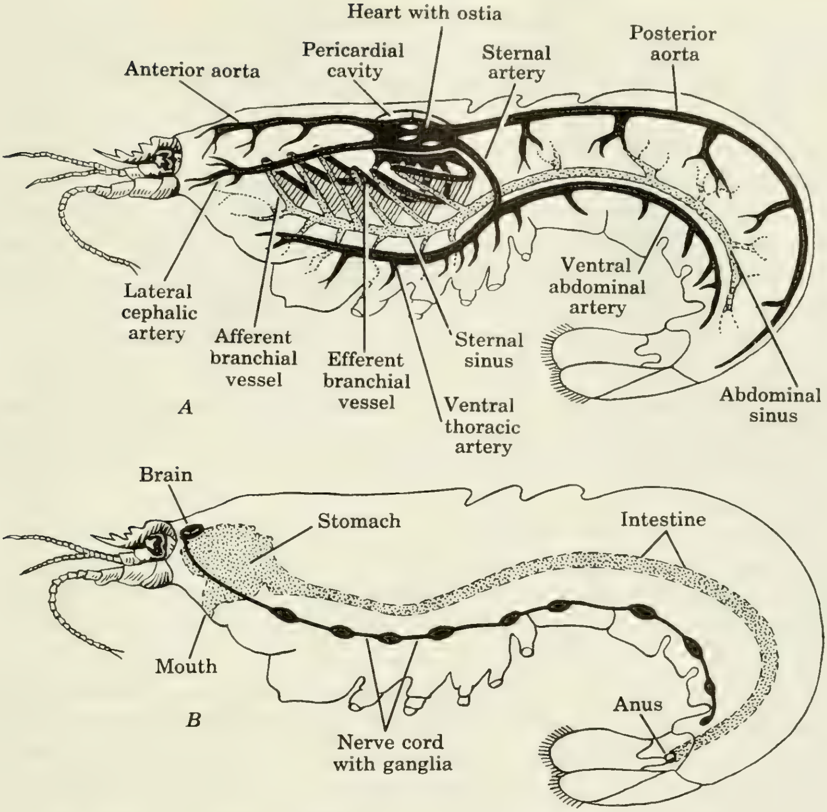

Heart with ostia
Posterior aorta
Pericardial cavity
Sternal artery
Anterior aorta
Lateral cephalic artery
Afferent branchial vessel
Efferent branchial vessel
Sternal sinus
Ventral abdominal artery
Ventral thoracic artery
Abdominal sinus
A
Brain
Stomach
Intestine
Mouth
B
Anus
Nerve cord with ganglia

Fig. 15.5. General relationship of the vascular, digestive, and nervous systems of the crayfish; semidiagrammatic. *A*, vascular system; distributing vessels are shown in black; collecting vessels and sinuses are stippled. *B*, digestive system (stippled) and nervous system (black); the large digestive glands, which occupy much of the space in the cephalothorax, have been omitted from this diagram. (Modified after K. von Frisch, 1952, *Biologie*, vol. 1, printed by permission of Bayerischer Schulbuch-Verlag.)

from endoderm during development. The remainder of the digestive tube is lined by tissues derived from ectoderm and is covered by a cuticle of varying thickness.

The digestive glands, and the viscera generally, are surrounded by extensive cavities through which blood flows after it has left the arteries (see p. 432). These cavities, because they contain blood, are collectively termed the **hemocoel.** They are not homologous with the coelomic cavities of other schizocoelous forms, although the true coelomic cavities of the embryonic stages may contribute slightly to their formation. More definitely identifiable remnants of the embryonic coelom are found as sacs at the inner ends of the excretory organs, and perhaps as the cavities within the hollow ovaries and testes.

The **circulatory system** of the crayfish, unlike that of such annelids as the earthworm, is not a "closed" system with capillaries. Rather, it resembles superficially the "open" circulatory system described for most mollusks. Branching arterial vessels conduct blood from the **heart** to the organs, where the arteries terminate (Fig. 15.5). Leaving the arteries, blood percolates through the tissues and collects in **sinuses,** or hemocoelic spaces. From the general hemocoel blood flows ventrally into the **sternal sinus** and the **lateral sinuses** with which the sternal sinus communicates. From the lateral sinuses a series of vessels constituting the **branchial circulation** carries blood through the gills for oxygenation. The blood then passes through a system of venous channels into the **pericardial sinus** surrounding the heart, and re-enters the heart, when it relaxes between beats, through three pairs of valved openings, the **ostia.** Such an "open" system is not markedly efficient; the pressure exerted by the heart in contraction is rapidly dissipated in the large sinuses, and blood flow through the gills is relatively slow.

Such a system obviously suffices for the needs of the animal, however. Blood flowing to the tissues transports to them food picked up in the digestive glands, and oxygen from the gills, and carries away carbon dioxide and nitrogenous wastes. Carbon dioxide is exchanged for oxygen in the branchial circulation, and nitrogenous wastes are removed from the blood in the excretory organs.

The gills and their circulation, which constitute the mechanism of **gas exchange,** have been adequately described. The efficiency of this mechanism is enhanced by the maintenance of an external water circulation over the gills. In the living crayfish water is continually drawn under the posterior and ventral edges of the carapace into the gill chambers, where it passes forward, bathing the gills, and is ejected anteriorly. These water currents are produced by a specialized, paddle-like extension of the second maxilla on each side of the body. As previously mentioned, the swimmerets aid by keeping the water in motion about the posterior, ventral part of the body.

The **excretory organs** are a pair of compound tubular structures termed the **green glands.** These lie in the hemocoel, one on each side, just anterior to the stomach. Each (Fig. 15.6) consists of a terminal, flattened **end sac,** a convoluted **labyrinth** or **cortex,** and a **distal tubular portion,** at least partially lined by secretory epithelium, leading from the labyrinth to a small **bladder.** The bladder opens externally by a **nephridiopore** on the basal segment of the antenna. The green gland is interpreted as a compound nephridium; the end sac is considered the remnant of a coelomic pouch. The blood supply to these organs is copious, derived from branches of the lateral cephalic and ventral thoracic arteries. The functions of the green glands are not completely understood. According to current interpretations, nitrogenous wastes and salts are extracted from the blood in the labyrinth and proximal parts of the tubule; as the urine thus formed flows outward through the tubule, secretory cells lining the distal portion selectively reabsorb salts and return them to the blood. The comparatively watery urine remaining in the tubule is then

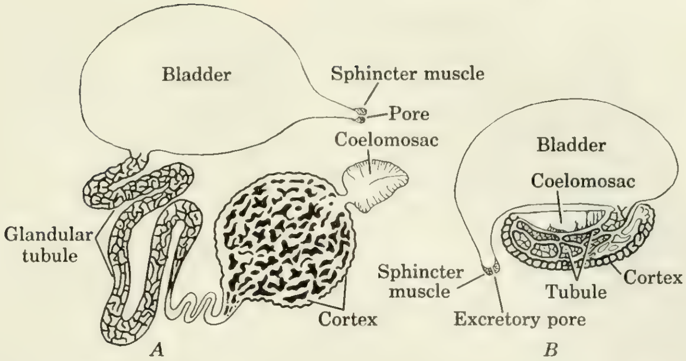


Fig. 15.6. Green gland of the crayfish; semidiagrammatic. *A*, the gland extended, showing relationships of the various portions. *B*, the gland in vertical section, as it lies in the hemocoel. (Redrawn from P. Marchal, 1892, *Archives de zoologie expérimentale et générale*, vol. 10.)

passed into the bladder, which empties periodically to the exterior. It is thus apparent that through the selective activities of the secretory tubular cells, the green glands are important not only in excretion but also in salt and water balance.

The Nervous System and Responsiveness. The general plan of the nervous system in the crayfish is similar to that of annelids (Fig. 15.7). There is a dorsal ganglionic mass, the **supraesophageal ganglion**, or "brain," from which nerves extend to the eyes and antennae. The brain also gives rise to a pair of **circumesophageal connectives** which pass around the esophagus and join with the **subesophageal ganglion** at the anterior end of the ventral **nerve cord.** Nerves arising from the subesophageal ganglion innervate the six pairs of oral appendages, the green glands, the esophagus, and the muscles of the anterior region of the thorax. In the course of embryonic development the subesophageal ganglion is formed by the coalescence of six pairs of ganglia, corresponding to the six pairs of oral appendages. The ventral nerve cord is a double structure, composed of fused, paired ganglia, joined together in a linear series by connectives. Posterior to the subesophageal ganglion there is a pair of ganglia for each somite; the metameric nature of the animal is thus revealed by the segmental organization of the nervous system, as well as by external divisions and the distribution of appendages.

The antennules and antennae bear very numerous receptors, for both tactile and chemical stimuli. In addition to these receptors, the hair-like processes upon the appendages and other parts of the body, such as the edge of the carapace, are tactile in function. Related to these tactile receptors are two **statocysts,** which are organs of equilibration located in the basal segment of each antennule. The statocysts are sac-like invaginations from the outer surface of the appendage; they are thus lined with an exoskeletal

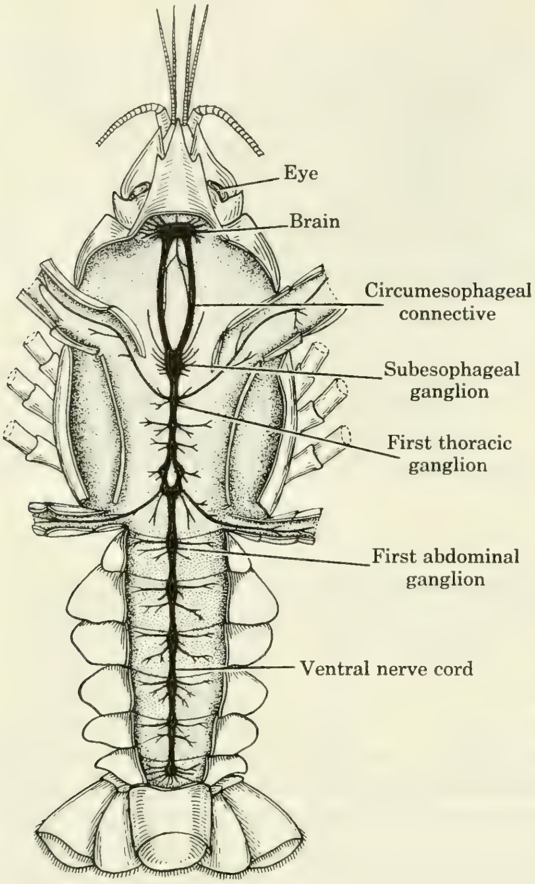


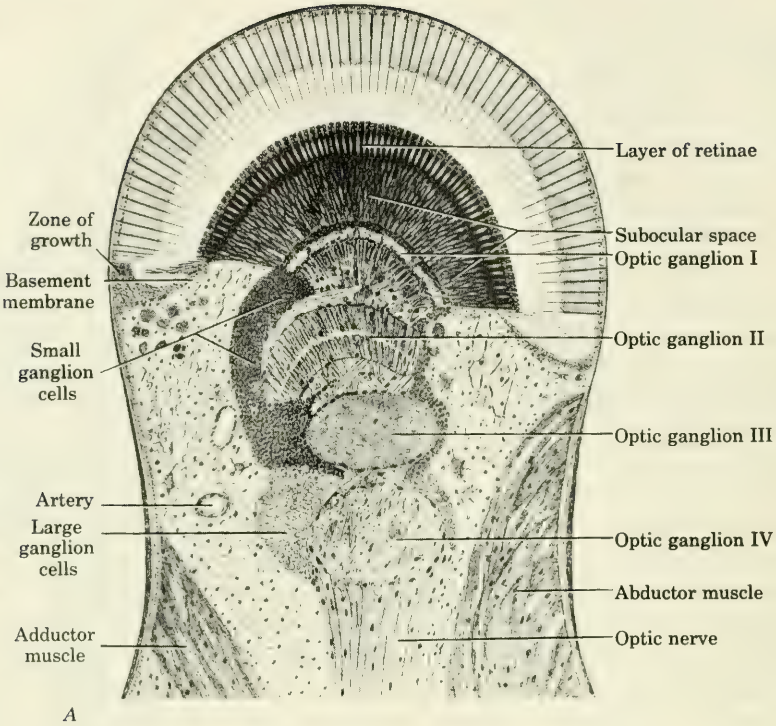
Fig. 15.7. Nervous system of a crayfish, *Astacus;* dorsal view. (Redrawn with modifications from W. Schmidt, 1915, *Zeitschrift für wissenschaftliche Zoologie,* vol. 113.)

layer, and the hairs projecting into their cavities are comparable with the sensory hairs on other parts of the body. Like the statocysts of other animals, these organs contain particles called **statoliths;** in the crayfish the statoliths are foreign bodies such as sand grains, which are lost at the time of molting and must be replaced from an external source. If a freshly molted crayfish is placed in water without such foreign particles, none can be found in the statocysts, and the animal shows disturbances in maintenance of equilibrium. If iron filings are supplied to such an animal, instead of sand grains, some of these may be worked into the statocysts; the animal's reactions can then be tested by subjecting it to a movable magnetic field. The reactions under such conditions verify the fact that the statocysts are organs of equilibration, and that sensory hairs in different parts of the organ are stimulated by contact with the statoliths as the animal changes its position with reference to the force of gravity. Nerve impulses set up by such stimulation pass to the brain, where appropriate reflex motor acts are initiated to maintain the animal's normal posture.

The chief **light receptors** of the crayfish are the paired **eyes**; each eye is borne on a movable stalk arising from the head. The eyes are of the compound type, made up of large numbers of individual units, the **ommatidia** (Fig. 15.8). Each ommatidium consists of a distal corneal structure, a lens-like refractile body, migratory pigment cells to adjust the intensity of light, and light-sensitive receptor cells which send nerve fibers toward the brain. Each ommatidium is thus a complete visual unit, capable of responding to its visual field. It is impossible to determine, however, whether the crayfish actually "sees" with its brain a mosaic of individual images or a composite single image. The compound eyes, from their structure, are well adapted for the detection of movement across the visual field, and this may be more significant in the life of the crayfish than actual image formation.

In the crayfish, as in other Metazoa, the function of the nervous system involves chiefly the short-term, rapid integration of the activities of the animal, or what might be termed **nervous coordination.** In recent years an increasing body of experimental evidence indicates that **chemical** or **hormonal coordination** also plays an important part in regulating the vital functions of the crustaceans generally. Certain glandular structures, notably the **eyestalk glands** and the so-called "Y-organs," in addition to groups of specialized **neurosecretory cells** in the central nervous system, produce specific chemical mediators, or hormones. These substances, released into the circulating blood, either directly or indirectly exert profound effects on the slower, cyclical changes in the body of the animal. Chemical coordination is involved in controlling the reversible color changes in the epidermis, in regulating the complex phenomena of the molting cycle, and in controlling various reproductive and metabolic cycles. The chemical mediators in crustaceans are analogous to the hormones produced in the endocrine glands of vertebrates (p. 117) and are apparently similar to the hormones of insects (p. 456).

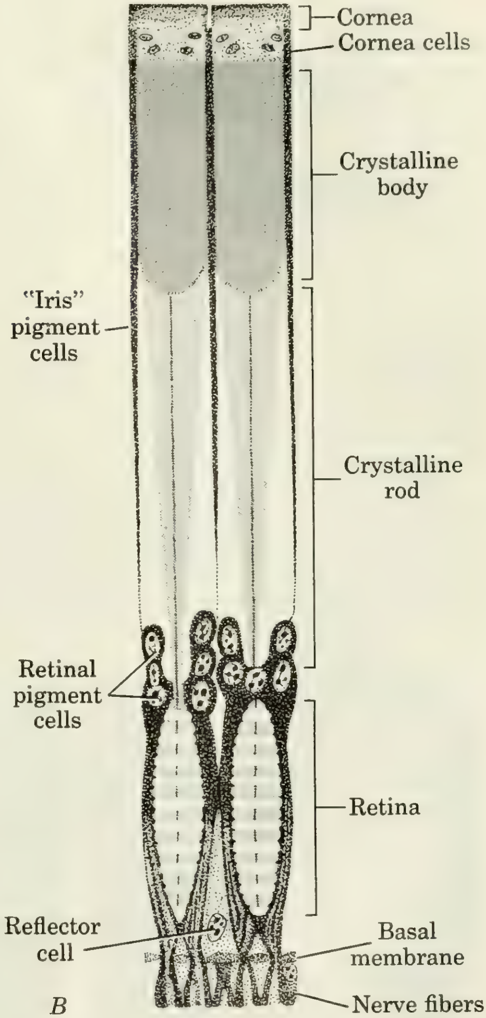
The Reproductive System, Reproduction, and Development. Crayfishes are dioecious; males and females may be distinguished externally by the structure of the first two pairs of swimmerets. Internally, the reproductive system consists of tubular gonads, **ovaries** or **testes,** which are paired anteriorly but unite below the heart to form a median, unpaired posterior lobe. The gonads lie in the thorax, dorsolateral to the digestive tract; the posterior lobe may extend into the first abdominal segment. The reproductive ducts of both sexes are paired, passing around the thoracic viscera laterally and ventrally to separate openings on the basal segments of specific thoracic appendages. The external openings of the **oviducts** lie on the third pair of pereiopods, those of the **ductus deferentes** (vasa deferentia) on the fifth pair. During copulation **spermatophores,** packets of spermatozoa bound together by mucous secretions, are emitted from the male genital openings. These packets are then transferred, by means of the modified swimmerets of the male, into the **seminal**


Layer of retinae
Zone of growth
Subocular space
Optic ganglion I
Basement membrane
Small ganglion cells
Optic ganglion II
Optic ganglion III
Artery
Large ganglion cells
Optic ganglion IV
Abductor muscle
Adductor muscle
Optic nerve
A

receptacle of the female. This is a pouch-like cavity lying between the bases of the fourth pair of pereiopods. The seminal receptacle has no internal opening; it serves merely to hold spermatozoa received at copulation until the subsequent time of oviposition. The large-yolked eggs, released from the oviducts, pass backward between the bases of the pereiopods and are fertilized by spermatozoa issuing from the seminal receptacle. The resulting zygotes are then attached to bristles on the swimmerets of the female. After hatching, the larvae remain attached to the swimmerets and develop through a series of molts until they have reached the stage of miniature adults and are able to begin an independent life.

Other Crustacea. According to older classifications, the class Crustacea was divided into only two subclasses, the **Entomostraca** and the **Malacostraca**. The Malacostraca, to which the crayfish, lobster, and other highly developed crustaceans belong, appears to be a natural grouping with distinctive characteristics. Thus, all the Malacostraca have a six- or eight-segmented abdomen, an eight-segmented thorax, abdominal appendages, and a gastric mill. In contrast, the Entomostraca of older authors constitute a heterogeneous assortment of crustacean types, many of them differing from one another as greatly as they differ from the malacostracans. We shall use the term Entomostraca descriptively, to refer to crustaceans which are small,

Fig. 15.8. The compound eye of the crayfish. *A*, longitudinal section of the entire eye, showing relationships of visual units (ommatidia), nerve tracts and their ganglionic relays, and the muscles by which the eye is moved. *B*, two adjacent ommatidia from an eye in the light-adapted condition; in dim light, the pigment in the "iris" pigment cells migrates distally and that in the retinal pigment cells moves toward the base. This removes the light barriers between the ommatidia and makes possible the formation of superposition images. (Adapted from H. Bernhards, 1916, *Zeitschrift für wissenschaftliche Zoologie*, vol. 116.)



aquatic, and generally of a simpler and more primitive organization than such forms as the crayfish.

The Entomostraca. The four principal types of entomostracans are represented by the orders Branchiopoda, Ostracoda, Copepoda, and Cirripedia. The majority of these are marine forms, although the Branchiopoda are predominantly fresh-water animals. The Branchiopoda include the fairy shrimps, such as species of the genus *Branchinecta* (Fig. 15.9). These animals swim on their backs, propelled by coordinated beating of their numerous, paddle-like thoracic appendages. Fairy shrimps occur typically in shallow, temporary ponds of fresh water formed in early spring by melting snow and may usually be found for only a brief period. The males of *Branchinecta* are

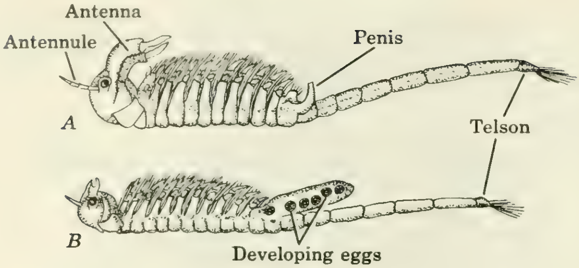


Fig. 15.9. Branchiopoda: the fairy shrimp, *Branchinecta paludosa*. *A*, male; *B*, female. (Redrawn, after A. S. Packard, from H. B. Ward and G. C. Whipple, *Freshwater Biology*, copyright 1918 by John Wiley and Sons, Inc., printed by permission.)

distinguishable from females by their second antennae, which are grotesquely modified as organs for clasping the female at the time of copulation. Fertilized eggs are carried for a time in a brood pouch on the ventral surface of the abdomen of the female. After these zygotes are released, they are very resistant to freezing and desiccation and so remain viable after the temporary ponds have dried up. These persistent zygotes produce the adults of the following spring, hatching as free-swimming **nauplius larvae** with three pairs of appendages and a single median eye. The adult arises from the nauplius through a series of molts, in the course of which the characteristic features

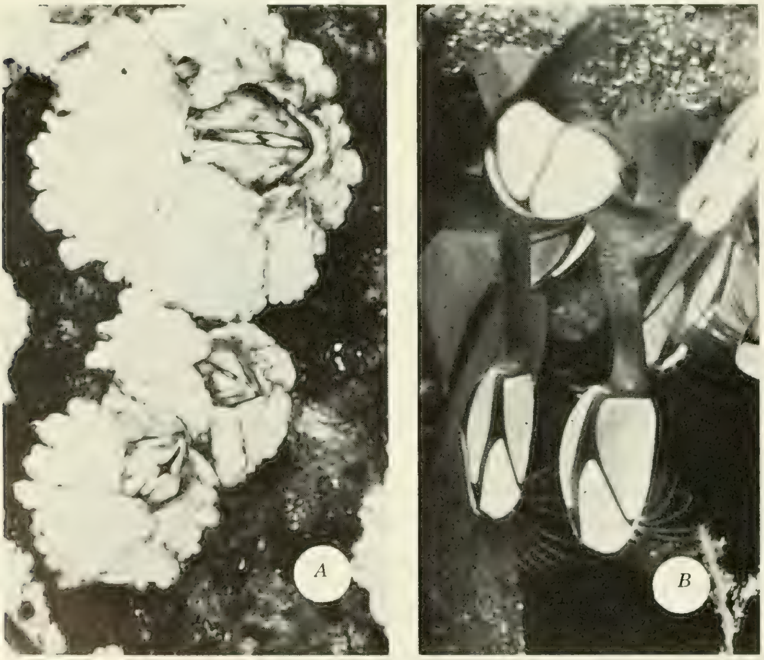


Fig. 15.10. Cirripedia. *A*, an encrusting barnacle, *Balanus*. *B*, a stalked or goose barnacle, *Lepas*. (Photographs by George Lower.)

are gradually acquired. Another branchiopod, *Artemia salina*, the "brine shrimp," is interesting in that it thrives in waters of extremely high salt concentrations. It is one of the relatively few animals able to tolerate conditions in the Great Salt Lake, and it also occurs in coastal brine pools in which sea water is evaporated to produce salt. The dried "eggs" of this species are sold commercially to biological laboratories and breeders of tropical fishes and will soon hatch to produce nauplii if placed in a strong salt solution.

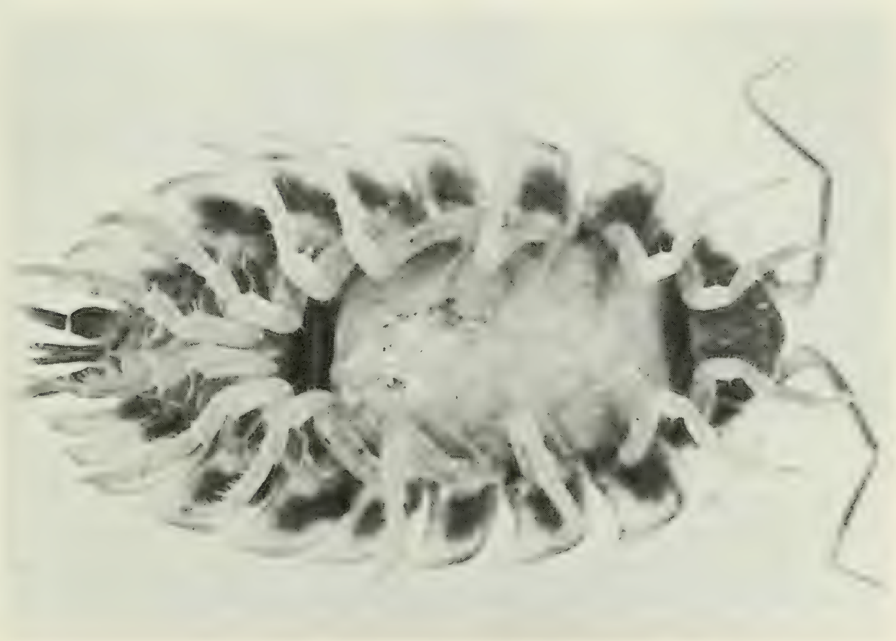
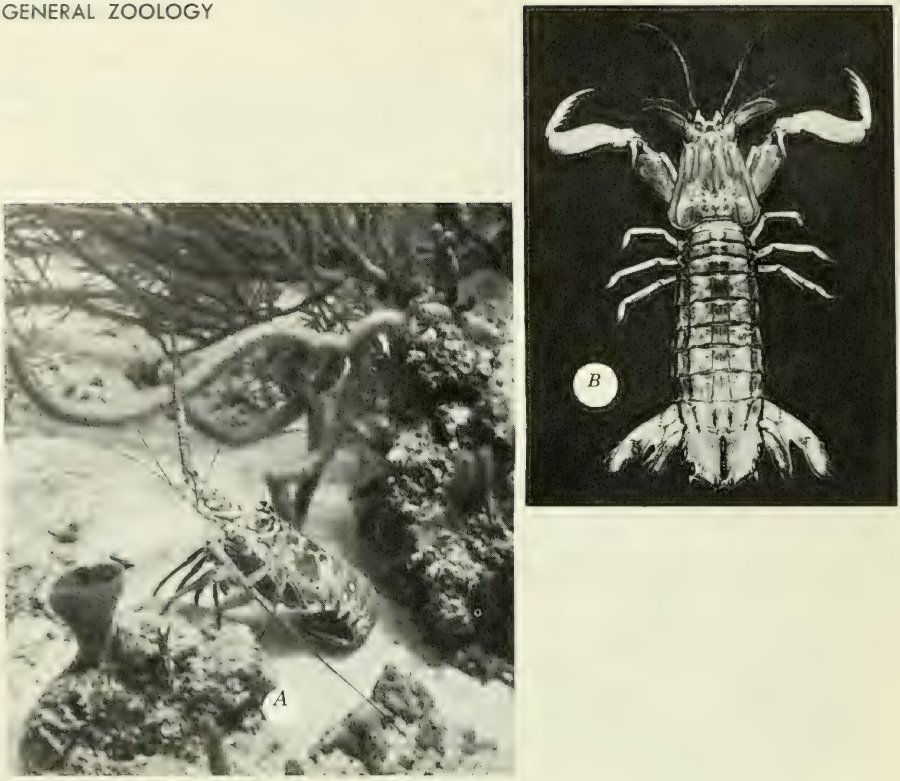


Fig. 15.11. Isopoda. A sow bug, ventral aspect. Note the relatively unspecialized nature of the segmental appendages. (Photograph by A. Smith, courtesy Department of Zoology, Cornell University.)

The Cirripedia, or barnacles, represent an extreme modification of the crustacean form in which the animal is attached during its adult life, though free-swimming as a larva. One type is the familiar rock barnacle, *Balanus*, found encrusting on rocks and shells between tide marks in the ocean (Fig. 15.10). Another type, *Lepas*, the "goose barnacle," is so called because of its long "neck," and because it was supposed by early naturalists to be the young of the wild goose. Goose barnacles are attached to the substratum by a fleshy stalk and are commonly found growing on floating timbers or masses of seaweed in deeper marine waters. During the change from larva to adult, barnacles become attached by the anterior end; the carapace is represented



by the calcareous shell plates, and the segmental appendages are highly modified for sweeping small particles and microscopic organisms from the surrounding water into the mouth. To paraphrase Huxley, we may think of the barnacle as a small shrimp-like animal, standing on its head in a little house, kicking food into its mouth with its feet.

The Malacostraca. These higher Crustacea include the forms popularly known as sow bugs, scuds, shrimps, prawns, crayfishes, lobsters, and crabs (Figs. 15.11, 15.12, 15.13). The great majority are marine animals, but many occur in fresh water; and a few, like sow bugs and the land crabs of the tropics, are terrestrial. The general characteristics of the typical malacostracan have been adequately described in connection with the crayfish and need not be repeated. Although internal organization is often modified in correlation with the habits of particular species, and external features are highly specialized in many instances, the fundamental plan of structure remains the same.

The crabs are examples of highly specialized malacostracans. In the familiar "blue crab," *Callinectes sapidus*, the eggs begin their development, as in the crayfish, attached to the abdominal appendages of the female. These eggs hatch, producing pelagic larvae of the so-called **zoaea** stage; these larvae drift with the plankton of the ocean, eventually transforming into a **megalops** form (Fig. 15.13). Interestingly, the zoaea larva, although it lacks a full comple-

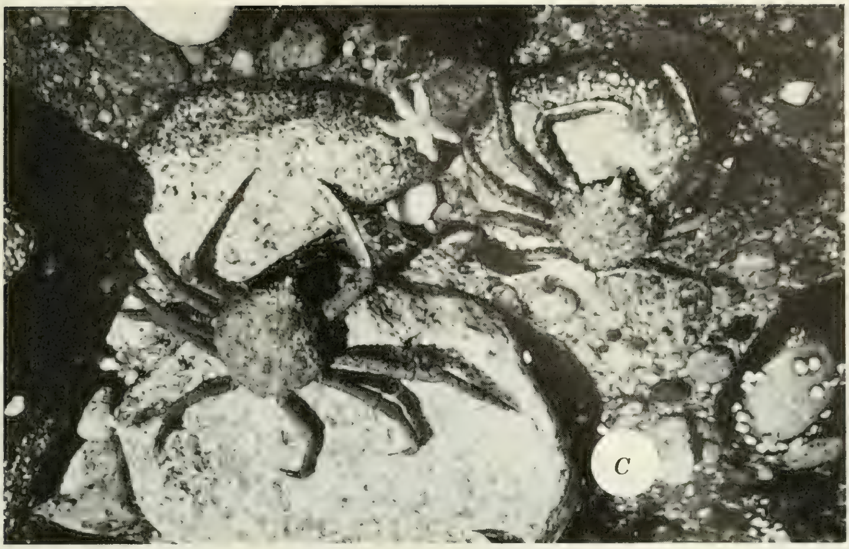


Fig. 15.12. Representative decapod crustaceans. *A*, the spiny lobster, *Panulirus argus*, in its natural tropical marine habitat; in this large decapod the first walking legs are not modified into powerful chelae like those of the American lobster, but the antennae are tremendously enlarged and elongated. *B*, the mantis shrimp, *Squilla empusa;* note the short carapace and the peculiar modification of the first walking legs for grasping prey. *C*, spider crabs, *Libinia emarginata;* in these non-swimming crabs the last segment of the fifth walking leg is a simple, pointed spine, not a broad paddle as in the swimming crabs (see Fig. 15.13). (*A*, underwater photograph by John F. Storr; *B* and *C*, photographs by Eugene S. Clark, Jr.)

ment of appendages and has some specializations for a drifting planktonic life, resembles in its general features a small crayfish or lobster. The megalops larva, however, begins to show a slightly crab-like form, with a somewhat broadened cephalothorax and a reduced abdomen. In the final transformation from larva to adult, the definitive form is assumed, with a relatively small abdomen folded forward under the greatly broadened and flattened cephalothorax. The blue crab is adapted for swimming by modification of the fifth pereiopods into paddle-like appendages; in many other crabs which do not swim, such as the spider crab, *Libinia* (Fig. 15.12), these appendages are simply pointed, as in the crayfish and lobster.

THE CLASS INSECTA

In numbers of known species, as well as in numbers of individuals, the Insecta are the dominant form of animal life upon the land. They are primarily and predominantly terrestrial animals; very few pass any part of their lives in the sea, and those that live in fresh water as immature forms or as adults are clearly typical insects especially modified for aquatic life. The most easily recognizable external features of insect structure are the division of the body into head, thorax, and abdomen; the two pairs of wings

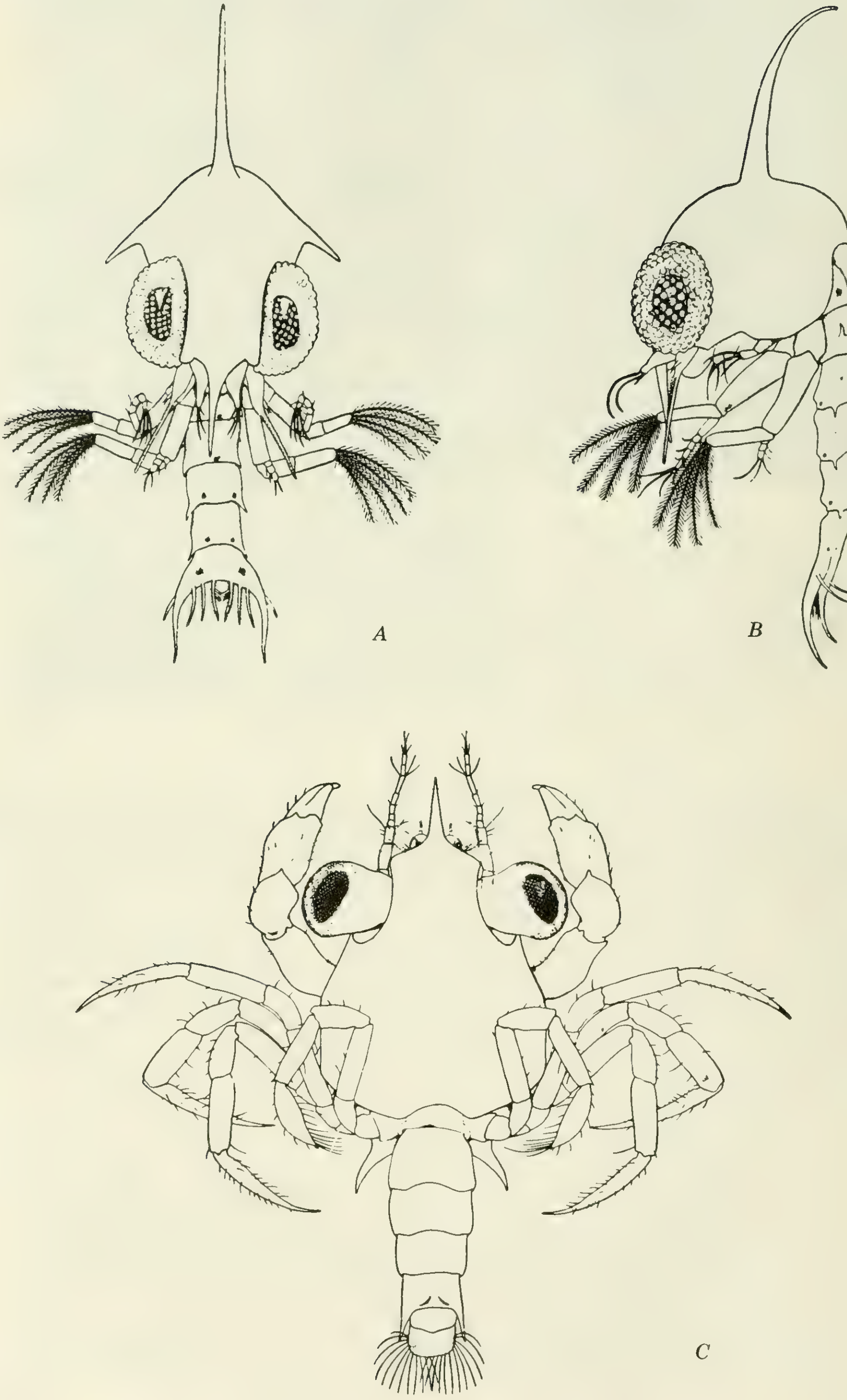
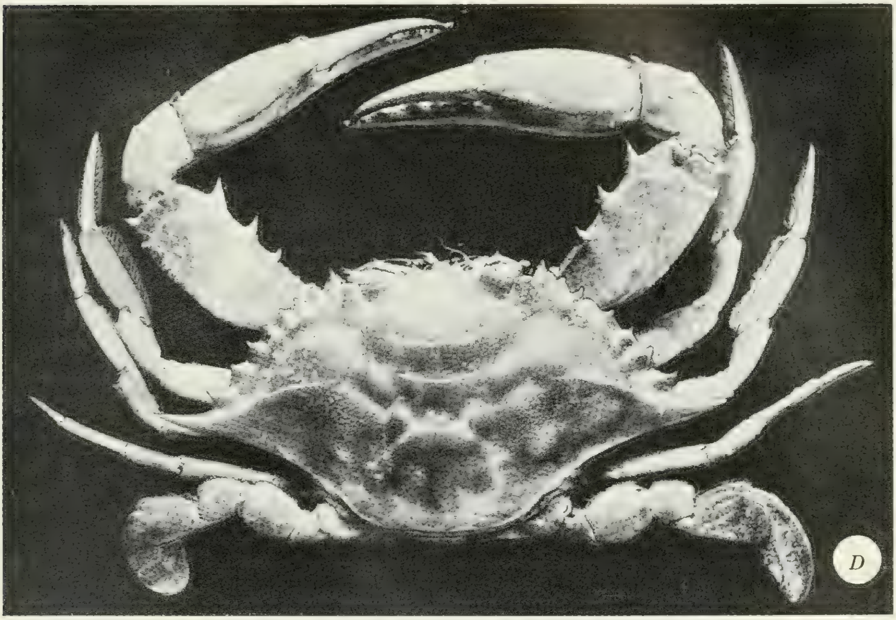

A
B
C

Fig. 15.13. The blue crab, *Callinectes sapidus*. *A* and *B*, ventral and lateral views of zoaea larva. *C*, dorsal view of the succeeding megalops stage. *D*, adult male, dorsal view. Note the shrimp-like proportions of the zoaea and the relative enlargement of the cephalothorax in the megalops. (*A*, *B*, and *C*, reproduced from E. P. Churchill, 1942, Chesapeake Biological Laboratory Publication No. 49, printed by permission; *D*, reproduced from M. J. Rathbun, 1896, *Proceedings of the U.S. National Museum*, vol. 18.)



and three pairs of legs borne upon the thorax; and the spiracles, which are the external openings of the system of air tubes, or tracheae, which distribute air to the tissues. Representatives of the order **Orthoptera**, which includes such generalized insect types as the locusts and grasshoppers (Fig. 15.14), will be described to illustrate the typical structural and functional aspects of the insects. We shall then consider certain fundamental phenomena in the metamorphosis and life cycles of insects and discuss briefly representatives of selected orders.

The Locust: ***Habitat and Activities.*** Locusts, often referred to as "grasshoppers," are universally distributed on all continents, in climates where insect life in open fields is abundant. They crawl upon the grass and other similar vegetation, leap into the air by means of their large posterior legs, and may actually fly if the wings are well developed. Their shrilling as they rest upon the ground, and the clacking of their wings in flight, are familiar

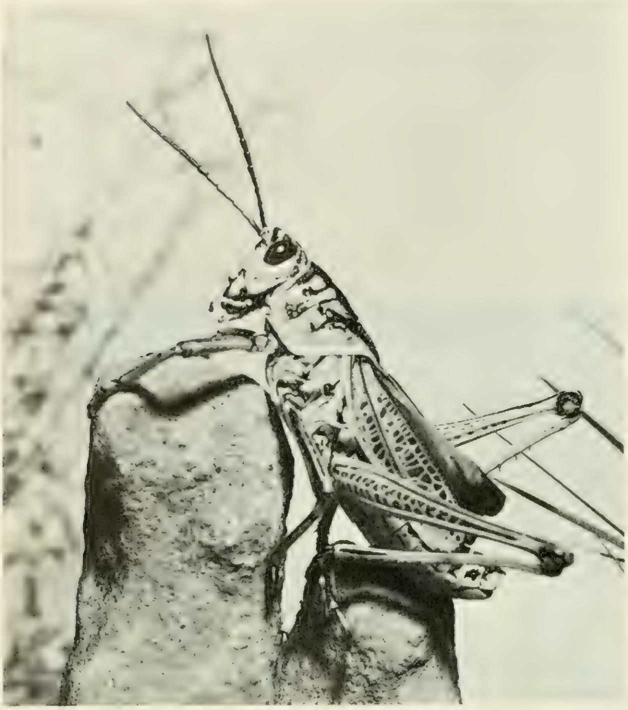


Fig. 15.14. The Eastern lubber locust, *Rhomalea microptera.* (Photograph courtesy New York Zoological Society.)

sounds of the day, just as the stridulations of their near relatives, the katydids and crickets, are among the most familiar nocturnal sounds. Some locusts are **non-migratory,** spending their entire lives in a single field. Other species, or other races of the same species, may be **migratory,** breeding in one locality and moving to another. In the migratory forms the young hatch in May or June, depending on climatic factors, and migration begins within a few hours. The animals move in great swarms; since the wings have not yet developed at this stage, the animals progress by hopping and by crawling rapidly over the ground. Crossing a cultivated field, the swarm consumes all the plants, even to the roots; yet it may pass on to barren land beyond, without destroying the growth of plants on either side of its line of travel. As the individuals in the swarm reach maturity and their wings become fully developed, the swarm can take to the air and move for miles in such numbers that they obscure the sun.

General Structure. The body is conspicuously divided into the three regions typical of insects: the **head,** the **thorax,** and the **abdomen** (Fig. 15.15). The abdomen shows eight well-defined segments, with portions of at least three additional posterior somites. There are, as in other insects, three thoracic segments, the prothorax, mesothorax, and metathorax, each bearing a pair of legs. The number of segments in the head is problematical, but there is clear evidence of at least four somites. The body is completely enclosed by the **exoskeleton**, which is firm in some regions but thinner and more flexible at the joints. Unlike the skeletons of many crustaceans, that of the locust is not hardened by depositions of calcium carbonate; it is composed of scleroproteins and chitin, covered at the surface by a thin waxy layer. As in other arthropods, an approaching molt is preceded by secretion of a new skeleton beneath the old one, through activities of the epidermal cells.

The head bears a pair of large **compound eyes** and three small simple eyes, or **ocelli** (Fig. 15.16). A single pair of **antennae** is present, bearing a great many sense organs. The antennae may be considered true segmental appendages that have been modified as sense organs, whereas the eyes and ocelli are primarily sensory structures and not appendages. The so-called "mouth parts" of the locust include segmental appendages as well as structures arising as median, unpaired outgrowths of the head (Fig. 15.17). The true appendages

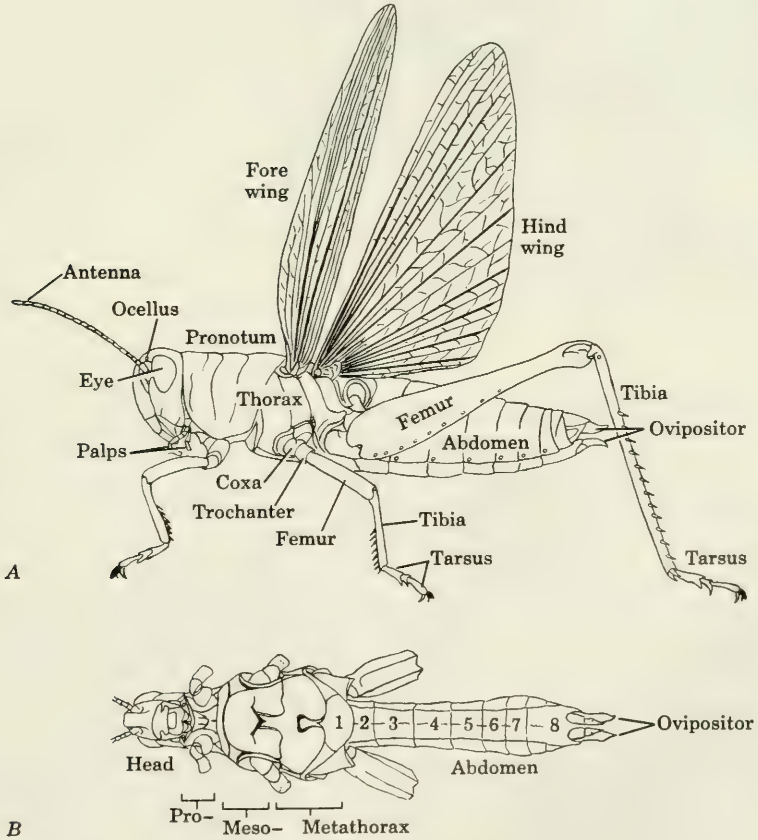

Fore wing
Hind wing
Antenna
Ocellus
Pronotum
Eye
Thorax
Femur
Tibia
Ovipositor
Abdomen
Palps
Coxa
Trochanter
Femur
Tibia
Tarsus
Tarsus
A
1
2
3
4
5
6
7
8
Ovipositor
Head
Abdomen
Pro–
Meso–
Metathorax
B

Fig. 15.15. General features of a locust, *Melanoplus differentialis*. *A*, female, lateral view; *B*, female, ventral view. (Redrawn from E. O. Essig, *College Entomology*, copyright 1942 by the Macmillan Company, printed by permission.)

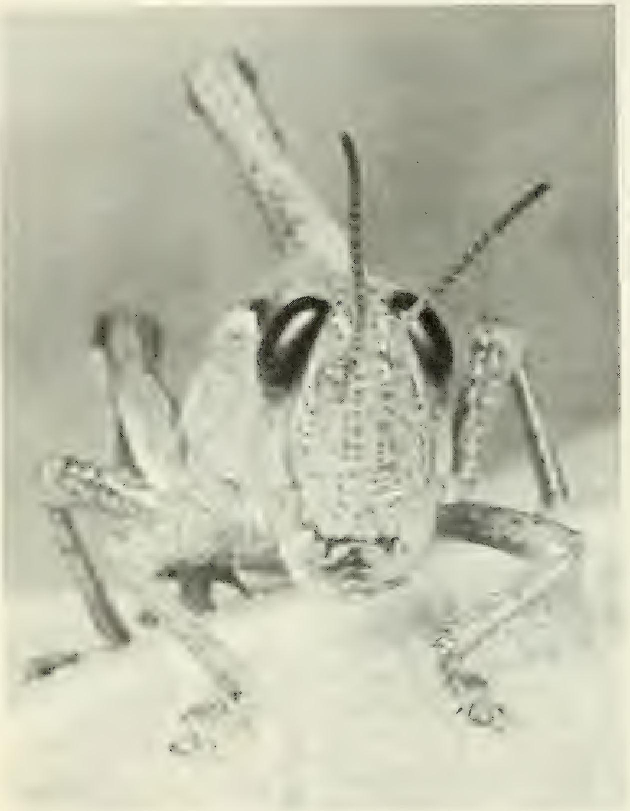


Fig. 15.16. Face view of a small locust. Note the prominent compound eyes and antennae, and the shield-like labrum covering the mouth parts anteriorly. (Photograph by Charles Walcott.)

are a pair of **mandibles**, or chewing jaws; a pair of **maxillae**, jointed, leaf-like structures modified to aid in the manipulation of food; and a single lower lip, the **labium**, which is derived during development by the fusion of a pair of second maxillae. The mouth parts which are not segmental appendages are the **labrum**, or upper lip, formed as a downgrowth from the anterior surface of the head, and the **hypopharynx**, a median projection from the floor of the mouth which acts more or less as a tongue. Possessing mandibles and other mouth parts adapted for chewing, the locust is spoken of as a **mandibulate** insect. As we shall see, in other insects the same fundamental mouth parts may be modified for sucking, for piercing and sucking, and for lapping; however, the primitive insects are believed to have been mandibulate.

Each of the three thoracic segments bears a pair of jointed appendages, the **legs**. These are all similar in structure, but the posterior or metathoracic legs are highly developed and specialized for leaping. At the distal end of each leg, a small pad and a pair of hooks provide grasping organs by which the insect obtains a firm hold upon vegetation. Two pairs of **wings** are attached to the dorsolateral surfaces of the mesothoracic and metathoracic segments, as in most other insects. In the locust the anterior wings are usually heavy and tough and function as protective covers for the delicate, membranous metathoracic wings. In the lubber locusts both pairs of wings are greatly reduced, with a corresponding decrease in the power of flight. The wings of insects are composed mainly of exoskeleton, with a very small amount of cellular material between the upper and lower skeletal layers. They are stiffened and supported by thickened structures, called "veins," between which the wing is thin and membranous. The veins also mark the pathways of channels through which blood circulates.

The abdomen lacks segmental appendages, and none appears in this region during development in the locust; in certain other insects there are traces of vestigial abdominal appendages in the embryonic stages, and these persist to adulthood in some small, wingless, primitive insects. In the female locust a large **ovipositor** is present at the posterior end of the abdomen, surrounding the external opening of the female reproductive system. In the male an eversible **penis** marks the opening of the genital duct, just ventral to the anal opening at the tip of the abdomen.

External openings of the **respiratory system** appear as the paired **spiracles**; one lies on each side of every thoracic segment and each of the first eight abdominal segments. In life, the spiracles are opened and closed rhythmically with the breathing movements of the body. The so-called **tympanic membranes**, which are the external parts of the auditory organs, are conspicuous structures like eardrums on the dorsolateral portions of the first abdominal segment of the locust.

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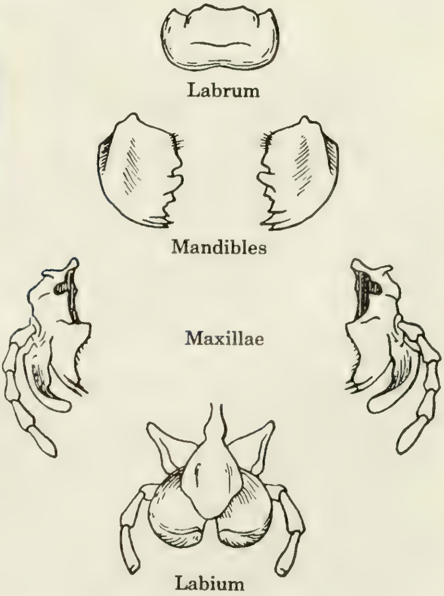


Fig. 15.17. Mouth parts of a locust. (Adapted from T. Dobzhansky, *Evolution, Genetics, and Man*, copyright 1955 by John Wiley and Sons, Inc., printed by permission.)

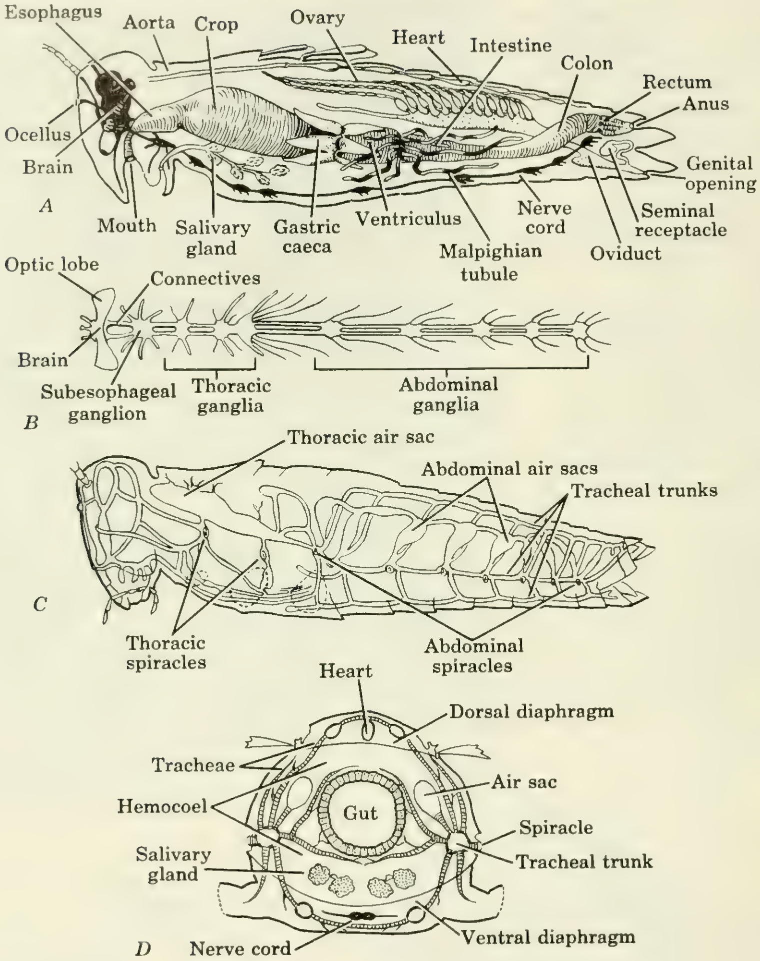

Esophagus
Aorta
Crop
Ovary
Heart
Intestine
Colon
Rectum
Anus
Ocellus
Brain
Genital opening
A
Mouth
Salivary gland
Gastric caeca
Ventriculus
Nerve cord
Seminal receptacle
Malpighian tubule
Oviduct
Optic lobe
Connectives
Brain
Subesophageal ganglion
Thoracic ganglia
Abdominal ganglia
B
Thoracic air sac
Abdominal air sacs
Tracheal trunks
C
Thoracic spiracles
Abdominal spiracles
Heart
Dorsal diaphragm
Tracheae
Air sac
Hemocoel
Gut
Spiracle
Salivary gland
Tracheal trunk
D
Nerve cord
Ventral diaphragm

Fig. 15.18. Details of some internal features of the locust. *A*, lateral view, showing relationships of digestive, reproductive, nervous, and excretory systems. *B*, major parts of the central nervous system, ventral view. *C*, major parts of the tracheal system. *D*, cross section of the body in the thoracic region; all cross-hatched structures are tracheal branches. (Adapted from E. O. Essig, *College Entomology*, copyright 1942 by the Macmillan Company, printed by permission.)

Structures and Functions Related to Metabolism. The internal anatomy is much the same in all species of locusts. The **digestive system** (Fig. 15.18) develops by specific modifications, extremely specialized in some insects, of an originally simple tube running from mouth to anus. Only the midregion of this tube, as in the crayfish, is lined by tissues derived from embryonic endoderm. The anterior and posterior regions are lined by inward extensions of the epidermis and are covered by cuticle, which is shed as the animal molts. The **buccal cavity,** enclosed by the mouth parts described above, receives the ducts from the **salivary glands** lying in the thorax. From the buccal cavity a short **esophagus** leads dorsally, widening to produce a thin-walled **crop** which extends into the thorax. The crop tapers posteriorly and joins the **stomach.** The junction between crop and stomach is marked by six pairs of glandular outgrowths of the digestive tract known as **gastric caeca;** these caeca secrete a juice containing digestive enzymes. Posterior to the stomach lies the **intestine,** which has a narrow region, the "colon," followed by an expanded **rectum** leading to the anus. The division between stomach and intestine is marked by the zone of attachment of the Malpighian tubules, which are excretory organs.

In feeding, the animal bites off pieces of grass and other vegetation with its mandibles, using the labrum and labium as upper and lower lips, and the palps of the maxillae and labium as tactile and gustatory organs. The salivary secretion, emptied into the buccal cavity, serves as a lubricant in swallowing and as a digestive fluid acting upon food stored in the crop. **Digestion** may occur to some extent in the crop, but the cavity of the stomach is the principal digestive region. **Absorption** of products of digestion into the circulating blood occurs in the stomach and the anterior part of the intestine, and **assimilation** follows the diffusion of these transported nutrients into the cells of the body.

As in the crayfish, the contribution of the embryonic **coelom** to the definitive body cavities of the locust is problematical. The spaces between muscles and surrounding the viscera are hemocoels and do not, on the whole, represent a modified coelom. In the adult locust this space is largely occupied by an irregular mass of storage tissue termed the **fat body.** Such fat bodies make up most of the body bulk in insect larvae storing up food reserves in advance of metamorphosis.

Leading from the spiracles on the thoracic and abdominal segments are the air tubes, or **tracheae,** which form the **respiratory system.** The tracheae unite and branch in a complex manner and expand into conspicuous reservoirs, or **air sacs,** in the abdominal region (Fig. 15.18). The fine end branches of the tracheae, the **tracheoles,** ramify within all the tissues of the body and permit the direct delivery of atmospheric oxygen to the fluids surrounding the cells. Air must first enter the body through the spiracles, a fact which makes it possible to kill insects by clogging these openings with dust or films of oil and soapsuds. Oxygen enters the cells of the insect from the intercellular fluid and is used, as in other animals, in cellular metabolism. The tracheal type of respiratory mechanism is found only among the higher arthropods and their relatives, the Onychophora. The fact that many insects are capable of rapid and sustained metabolic activities, as in prolonged periods of flight, is an indication that the tracheal system has been developed to a high point of efficiency.

Malpighian tubules are the chief **excretory organs** of insects, functioning to remove nitrogenous wastes of metabolism from the blood and eliminate them from the body. Each tubule, of which there may be dozens or hundreds, is

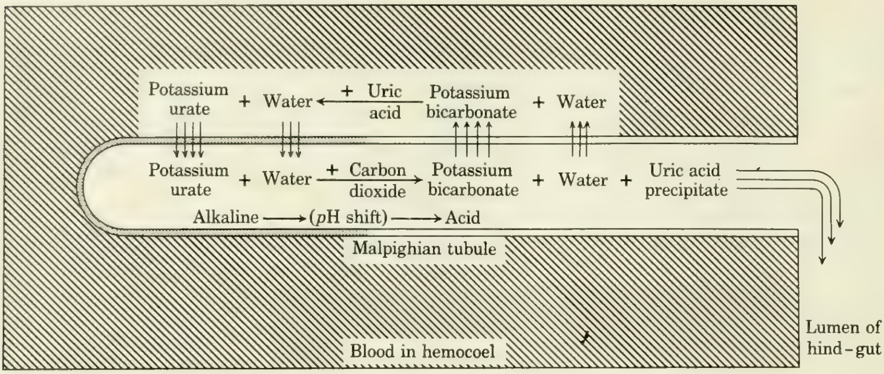


Fig. 15.19. Schematic diagram of the general mechanism of uric acid excretion in the Malpighian tubules of insects, based on the blood-sucking bug *Rhodnius*. (Adapted from V. B. Wigglesworth, 1931, *Journal of Experimental Biology*, vol. 8, printed by permission.)

composed of large cells surrounding a tubular lumen. The tubule is closed at its distal end, but the proximal end communicates with the lumen of the intestine. It is generally spirally wound about by several strands of muscle fibers. The tubules lie in the hemocoel, bathed by blood, from which the cells extract wastes, chiefly in the form of salts of uric acid (Fig. 15.19). These salts are passed through the wall of the tubule into the lumen and move downward, in solution, toward the intestine. Cells in the more proximal portions of the tubule extract water and certain inorganic constituents from this "urine," resulting in the precipitation of uric acid as crystals or concretions in the lumen of the tubule. By gentle muscular pulsations of the tubule, the precipitated mass, in the form of a paste, is emptied into the lumen of the hind-gut. Here more water is extracted, and the wastes are eliminated from the body with the feces. This excretory mechanism may be interpreted as an adaptation for the conservation of water, by eliminating wastes with the smallest possible loss of water.

The development of the tracheal system has relieved the blood of a function which in most other animals is of major importance, that of distributing respiratory gases. Consequently, it is not surprising to find that the **circulatory system** is not extensively developed, and that the flow of blood is relatively sluggish. The **heart** of the locust is a slender, pulsatile tube extending along the dorsal midline of the abdomen (Fig. 15.18). In each segment throughout its length, the heart is provided with a pair of valved openings, or **ostia.** The heart is supported from the dorsolateral body wall on each side by fan-shaped groups of **alary muscles** and lies in a division of the hemocoel termed the **pericardial sinus.** This space is separated from the perivisceral hemocoel by a perforated membrane, the **dorsal diaphragm.** Blood enters the heart from the pericardial sinus through the ostia and is driven forward, into the thorax and head, through the **aorta,** which terminates near the brain. From the head, blood flows posteriorly through the hemocoelic spaces, bathing the tissues, until it again reaches the abdomen, passes through the dorsal diaphragm, and re-enters the pericardial sinus and the heart. There is a variety of colorless, amoeboid cells in the blood of insects, but nothing comparable to the erythrocytes of vertebrates; the blood contains no pigments involved in the transport of oxygen.

The Nervous System and Responsiveness. The **nervous system** of the locust is arranged according to the typical arthropod plan, as described for the crayfish. There is a compound ganglionic mass in the head, termed the "brain" or **supraesophageal ganglion;** a pair of **circumesophageal connectives;** a **subesophageal ganglion;** and a ventral chain of paired, segmental ganglia with their connectives and radiating nerves (Fig. 15.18). The brain lies in the head between the compound eyes. Although it is obviously a compound structure produced by fusion of segmental ganglia, the exact number of such ganglia included cannot be determined. Large optic nerves pass into the brain from the compound eyes, smaller nerves from the ocelli, the antennae, and the labrum. In addition, small nerves extend ventrally to the **frontal ganglion,** from which the visceral or sympathetic nerve leads to the anterior part of the digestive tract. The circumesophageal connectives pass around the digestive tract and join the **subesophageal ganglion.** This also has a compound origin, apparently being formed during development by the coalescence of three pairs of segmental ganglia. From the subesophageal ganglion nerves radiate to the mandibles, the maxillae, and the labium. The thorax contains three paired ganglia, corresponding to the three thoracic somites. But the posterior ganglion is comparatively large, and its nerves are distributed in a way that indicates its formation by fusion of the third thoracic and first abdominal ganglia. There are five ganglionic masses in the abdomen, which again represent fusions, particularly at the posterior end of the nerve cord. The adult locust, therefore, has fewer ganglia than somites, but in the embryo there is a ganglion for each somite, as in the less highly specialized arthropods.

Like the majority of other insects, locusts are well equipped with **sense organs.** Small receptors for tactile stimuli are widely distributed over the surface of the body, and they are concentrated in especially sensitive areas, such as the antennae, the cerci at the tip of the abdomen, some of the mouth parts, and the distal segments of the legs. Olfactory stimuli also affect the basal parts of the antennae. Some insects are able to respond to very slight olfactory stimuli. For example, the males of certain species of moths will fly upwind from considerable distances in response to odors emitted by the scent glands of the females. Gustatory stimuli are perceived by taste organs on the mouth parts of the locust. The **ocelli** are sensitive to light but are probably incapable of forming images. When the **compound eyes** of a locust are covered with black paint, the insect will not react to moving objects by leaping away, but it will find its way out of a box in which there is only one small opening to admit light. When the ocelli as well as the compound eyes are covered, the animal escapes from the box only by chance. It has been shown that some insects respond differently to different wavelengths (i.e., colors) of light, although the range of stimulation is not the same as that in humans. Ants, for example avoid violet light, as they avoid direct sunlight, and they seem not to distinguish red or orange light from darkness. Ants and honeybees are very sensitive to ultraviolet light, but humans have no conscious perception of light in this portion of the spectrum. The structure of the compound eye in the locust is similar to that described for the crayfish (p. 435). Each eye consists of a large number of visual units, the **ommatidia,** each of which is capable of stimulation by light from a portion of the entire visual field. Eyes of this type, as previously noted, seem especially well adapted to the perception of moving objects, which stimulate different ommatidia in succession.

In the locust, the **tympanic membranes** are assumed to be auditory organs, more because of their structure than from any experimental evidence. Each consists of a membrane, against the inner side of which lie structures connected with nerves. Individual locusts react to, and so presumably "hear," the rattling sound produced by the wings of other locusts in flight. Comparable flight sounds are characteristic of many other insects; the buzz of a fly and the telltale whine of a mosquito are of this nature. The flight sounds of mosquitoes appear to be important in mating; recordings of the sounds emitted by females in flight have been shown to attract males in considerable numbers. The auditory organs of mosquitoes are located on the antennae.

The most conspicuous anatomical feature of the neurosensory mechanism in insects is the degree of **cephalization**—the concentration of the sense organs and ganglia with their adjustor neurons toward the head or cephalic end of the animal. This fact is obviously correlated with the very active life of most insects, which subjects them to frequent and varied changes in their environments; the condition resembles the more pronounced cephalization that characterizes the vertebrates. Insects exhibit reflex actions of great complexity, involving what have been called chain reflexes in vertebrates. Many of the activities which will be mentioned in discussing other groups of insects will illustrate this statement. There is no evidence that insects have any capacity comparable to the intelligence of higher vertebrates, although they perform instinctively very involved actions, especially in connection with mating, care of young, and colonial life.

The Reproductive System, Reproduction, and Development. In the account of external features the differences between male and female locusts have been described. Such differences in external characteristics are reflected in the internal details of the reproductive systems (Fig. 15.18). In the male there are two **testes,** which lie as a saddle-shaped mass dorsal to the intestine. The tubules leading from the testes pass ventrolaterally and unite into right and left **ductus deferentes** (vasa deferentia), which join at the midline beneath the intestine to form a single **ejaculatory duct** traversing the penis. **Accessory glands,** which open into the anterior end of the ejaculatory duct, secrete a fluid apparently necessary to aid the transfer of spermatozoa from

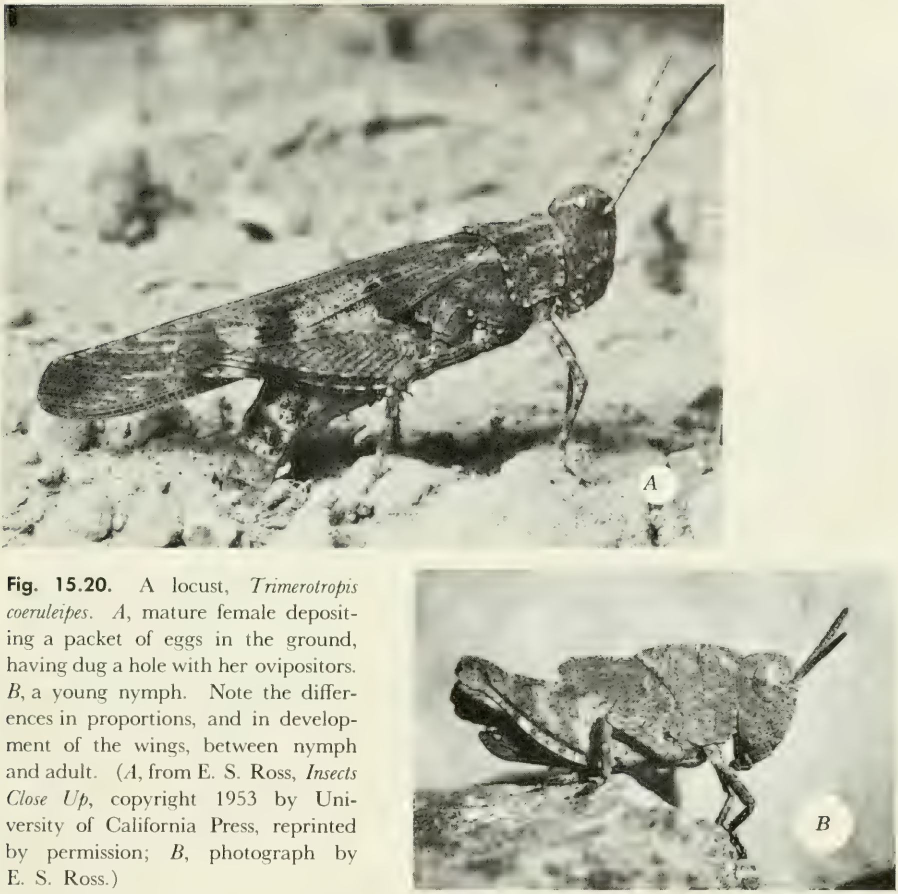


Fig. 15.20. A locust, *Trimerotropis coeruleipes*. *A*, mature female depositing a packet of eggs in the ground, having dug a hole with her ovipositors. *B*, a young nymph. Note the differences in proportions, and in development of the wings, between nymph and adult. (*A*, from E. S. Ross, *Insects Close Up*, copyright 1953 by University of California Press, reprinted by permission; *B*, photograph by E. S. Ross.)

male to female at copulation. In the female there are two **ovaries**, lying in a position corresponding to that of the testes in the male. Each ovary is composed of large numbers of tubular **ovarioles** in which the **ova** are formed. The ovarioles have a common anterior origin in the ovarial ligament, and all the ovarioles of each side unite posteriorly to form an **oviduct**. Passing ventrally like the ductus deferentes of the male, the two oviducts join beneath the intestine into a median tube, the **vagina**, which opens externally between the valves of the ovipositor. A small, tubular appendage of the vagina, the **seminal receptacle**, receives and stores spermatozoa transferred by the male at copulation. At the time of oviposition, eggs pass singly down the oviducts and through the vagina; as they move past the opening of the seminal receptacle, they are penetrated by spermatozoa from the stored supply and so leave the vagina as zygotes. The female deposits these zygotes, called "eggs," in masses of several dozen, placing them in the soil in holes dug beneath the surface by thrusting movements of the abdomen and ovipositor (Fig. 15.20). In

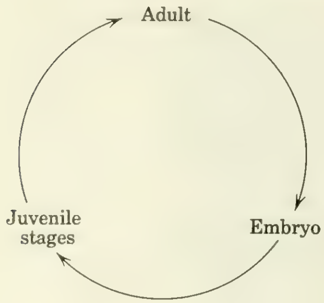


Fig. 15.21. Life cycle of an ametabolous insect.

temperate climates most species of locusts lay their eggs during late summer and autumn. The eggs undergo a period of dormancy, or **diapause**, and resume development only after they have been subjected to low temperature. Thus, the young do not normally hatch until the following spring. At hatching, the young locust, or **nymph**, resembles the adult, although the head is relatively larger and the wings are very small (Fig. 15.20). The final size and normal adult proportions are reached through a series of molts.

Insect Life Cycles and Metamorphosis. The life cycles characteristic of different insects range from very simple to extremely complex. Insects that on other evidence are considered among the most primitive in existence show what is probably the ancestral type of development. Eggs hatch to produce young which are exactly like the adults, except that they are smaller and are incapable of sexual reproduction. Increase in size and development of sexual maturity occur during a series of successive molts. Such a simple life cycle, which does not include **metamorphosis** (change of form), is spoken of as **ametabolous** (Fig. 15.21).

A different type of life cycle is characteristic of many insects such as locusts, which are not so primitive but are of rather generalized form. The young emerging from the eggshell is like a miniature adult in most respects, but its proportions are different, and the wings are relatively undeveloped. This immature individual is termed a **nymph**, which, like the young locust, gradually develops wings and attains adult proportions through a series of molts. This

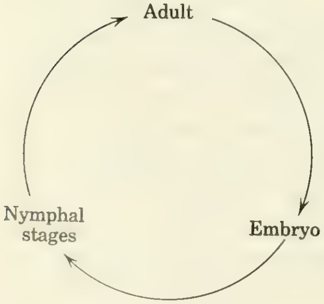


Fig. 15.22. Life cycle of a paurometabolous insect.

type of cycle, involving a **gradual metamorphosis**, is spoken of as **paurometabolous** (Fig. 15.22).

Somewhat different from the paurometabolous forms are those insects whose eggs are laid in water and develop into **aquatic nymphs**, or **naiads**. These immature forms are strikingly different from the adult and usually possess accessory structures, such as tracheal gills, related to their aquatic habitat. During its aquatic life the naiad increases in size by repeated molts; at maturity it crawls out of the water and in a final molt becomes the winged adult. This cycle includes a **partial metamorphosis** and is termed **hemimetabolous** (Fig. 15.23).

The most highly evolved insects, belonging to what may be considered the most successful modern orders, have the most complex life cycles. The young emerge from the eggs as **larvae**, which are completely different from the adult in structure, in habitat relations, and very often in food habits and feeding mechanisms. The larva, primarily a feeding stage, stores up reserves of energy in its fat body and other tissues in the form of fats and glycogen. After passing through a definite number of stages, each ending with a molt and an increase in size, the larva transforms into a resting stage, the **pupa**. At the conclusion of the molt marking the transition from larva to pupa, the general outlines of the adult body form are laid down and are often visible externally. The pupal stage may be brief, or it may last for several months. During this period the insect does not feed, and nothing enters or leaves the body except water vapor and respiratory gases. The pupa lives at the expense of reserves laid down during the larval stages, and after a longer or shorter period of quiescence, the organs of the adult begin to form. These structures are synthesized from stored reserves and from materials that become available as the special organs and tissues of the larva disintegrate. Eventually, the pupal skin splits, and the adult which has been formed within it emerges. This adult often has very small but perfect wings, which must immediately be inflated to full size and allowed to harden before they can be used. One of the first acts of the adult is the ejection from the anus of a mass of nitrogenous

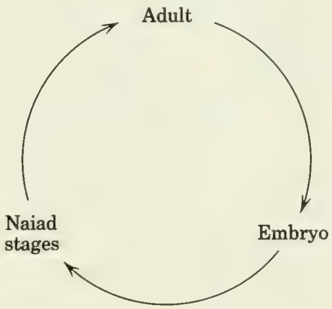


Fig. 15.23. Life cycle of a hemimetabolous insect.

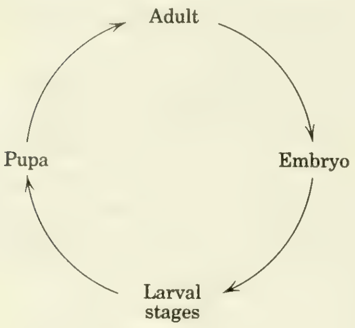


Fig. 15.24. Life cycle of a holometabolous insect.

wastes, representing excreta which have accumulated during the period of pupal life. The life cycle just described, consisting of embryonic, larval, pupal, and adult stages and including **complete metamorphosis,** is of the **holometabolous** type (Fig. 15.24).

Consideration of the life cycles of insects raises significant questions concerning the controlling influences regulating the far-reaching sequential changes involved in molting and metamorphosis. We have already noted (p. 435) that molting and other important systemic processes in the crayfish, and in crustaceans generally, are under the control of hormonal substances, produced by certain neurosecretory cells and transported by the circulating blood. Analysis of the processes of molting and metamorphosis in insects has shown that an analogous mechanism of control operates in these animals. In general terms, a group of neurosecretory cells in the brain of the insect secretes a hormone which acts specifically to activate a structure termed the **prothoracic gland,** apparently homologous with the "Y-organ" of crustaceans (p. 435). The prothoracic gland, in turn, produces a hormone which sets in motion the complex processes of growth and differentiation which lead to molting. A third endocrine organ, the **corpus allatum,** produces a conservative factor which has been termed the **juvenile hormone,** the general effect of which is to prevent changes of form at molting. In the presence of this last factor, a nymph molts to become a larger nymph, not an adult; and a larva transforms into a larger larva, not a pupa. At certain times in the life cycle, the corpus allatum ceases to produce its hormone, and in paurometabolous insects the adult stage is attained; in holometabolous forms pupation occurs.

A correlation between cyclical climatic changes and the timing of events in the life cycle is evident in many insects. For example, in many moths pupation occurs in late summer, and the pupa remains dormant until the following spring, when metamorphosis takes place. In some species it can be demonstrated that pupal dormancy continues indefinitely unless the insect is exposed to low temperature for a sufficiently long period of time. Low temperature, then, exerts some effect which sets in motion the initial steps in the process of metamorphosis. It has been established experimentally that the specific effect of low temperature is to activate neurosecretory cells in the brain of the pupa, causing them to secrete the hormone which stimulates production of the prothoracic gland hormone; this, in turn, initiates development of the adult insect within the pupal skin.

Students of insect physiology are actively investigating such fundamental questions as the evolution of these control mechanisms among insects in general, the precise biochemical foundations of endocrine regulation of metamorphosis, and related problems.

Representative Orders of Insects. Opinions differ about the number of orders among which the members of the class Insecta should properly be distributed. The number generally recognized varies approximately between twenty and thirty. In this section we shall describe and discuss briefly only a few of these orders, selected as illustrating the features of both simple and more complex insects. Additional details concerning these and other orders can be found in textbooks of entomology.

It will be noted that the features most commonly used in distinguishing between orders are (1) kind of life cycle; (2) nature of the wings, where these are present; and (3) differentiation of the mouth parts for different methods of feeding. A comparison of the various orders shows that the more generalized types of insects possess **mandibulate** mouth parts. In those which have developed other methods of feeding, involving perfection of **suctorial** mouth parts, the modified feeding apparatus is clearly derived from the more primitive mandibulate plan. In the simplest insects, such as Protura and Thysanura, wings are absent in the immature as well as in the adult stages; these and other wingless forms are sometimes grouped together as the **Apterygota.** Other insects are wingless as adults but show, by the appearance of abortive wing rudiments in the larval stages, that they have evolved from winged ancestors. The presence of two pairs of functional wings is characteristic of the **Pterygota,** comprising the majority of modern insects. In Coleoptera, and to a lesser extent in Orthoptera and Hemiptera, the anterior wings are specialized as protective covers for the hind wings. This, like the reduction of the posterior pair of wings in the Diptera, is regarded as a modification of the more typical four-winged state. As previously stated (p. 454), the simple, ametabolous life cycles of primitive insects indicate that the more complex cycles of higher orders have developed with the evolution of the class.

Order Protura (first tail)—minute, wingless forms living in humus and decaying leaves (Fig. 15.25). These must be considered the most primitive of living insects; although they possess a well-defined thorax and three pairs of legs, they are without antennae, the anterior pair of legs being held in front of the head as tactile organs. Unlike the more typical insects, proturans possess vestigial appendages on the anterior abdominal somites. In the course of growth to maturity, new somites are added at the posterior end of the body; this kind of growth is not typical of insects generally but is found in more primitive arthropods and in annelids. The mouth parts of proturans are mandibulate, and the life cycle is ametabolous.

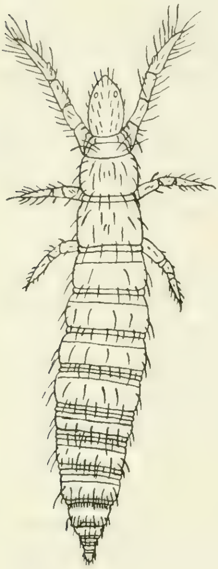


Fig. 15.25. Protura. A typical proturan, *Acerentulus barberi*. Note the simple eyes and the absence of antennae. (Redrawn, after H. E. Ewing, from H. H. Ross, *A Textbook of Entomology*, second edition, copyright 1956 by John Wiley and Sons, Inc., printed by permission.)

Order Thysanura (tassel tail)—generalized, wingless insects, some species of which possess such primitive characteristics as vestigial abdominal appendages and paired external genital openings. Common examples are the household pests known as silverfish, and the firebrat, *Thermobia* (Fig. 15.26). The mouth parts are mandibulate, and the life cycle is ametabolous.

Order Isoptera (equal wings)—termites. These primitive insects are interesting from several biological standpoints, as well as from the economic point of view related to their wood-eating habit and the consequent damage to houses and other wooden structures. The termites are primarily tropical forms but occur in warm temperature regions also. We have mentioned (p. 243) the array of hypermastigote flagellates which inhabit the intestinal tracts of termites and other wood-eating insects; this appears to be a mutual relationship, the insect depending on the capacity of the protozoans to digest cellulose. Although termites are structurally relatively simple insects, they have developed a social structure which to some extent parallels that of the social Hymenoptera (pp. 470–475). The social unit, or colony, is organized about a pair of functional reproductive individuals, the king and queen, responsible for the production of all the zygotes that develop into members of the society. In addition, there are variable numbers of sterile soldiers, or both sterile soldiers and sterile workers, and larger numbers of nymphs. Each of these **castes** exhibits morphological and behavioral specializations related to the maintenance of the colony. Experimentation has demonstrated that the numbers in each caste are maintained in constant ratio, and that the factors responsible for this coordination include specific substances which are transmitted between individuals. Briefly, some of the evidence is as follows. Normally, the presence of a royal pair inhibits the development of additional reproductive individuals, except in parts of the nest distant from the royal chamber. This inhibition appears to depend on the production by the king and queen of specific substances which all members obtain by ingesting the secretions or feces of the royal pair. If a colony is deprived of its king or its queen, supplemental reproductive individuals of the appropriate sex will develop within a short time, from among the undifferentiated nymphs. If an "orphaned" colony is separated from a normal one by wire screens which prevent all contact and all transfer of secretions, the isolated group will develop reproductive individuals in the normal manner. If only a single screen separates the groups, however, preventing transfer of secretions but allowing the members of the two colonies to touch each other with their antennae, the orphaned colony will develop supplementary reproductive individuals but kill them as fast as they are produced. Thus it is evident that caste development is regulated by two sets of stimuli, one sensory, the other chemical; it also appears that the two media of information transfer operate at different levels. Similar experimentation indicates that the same kinds of cues regulate colonial organization among other social insects such as bees, wasps, and ants.

In termites, as in ants, wings are developed by reproductive individuals in preparation for a seasonal swarming period. After the establishment of a new colony, the wings are discarded.

The mouth parts of termites are mandibulate, and the life cycle is paurometabolous, with gradual metamorphosis.

Order Odonata (toothed)—dragonflies and damsel flies. These are aquatic during the nymphal or naiad stages but give rise to aerial adults; the life cycle is thus hemimetabolous (Fig. 15.27). There are two pairs of membranous wings in the adult, and the mouth parts of all stages are mandibulate.

Adult dragonflies are wonderfully efficient fliers, skimming and hovering gracefully over the surface of ponds and streams. Although superstitiously considered dangerous to man, they are in fact beneficial, destroying innumerable small flies and mosquitoes which they capture in flight. The

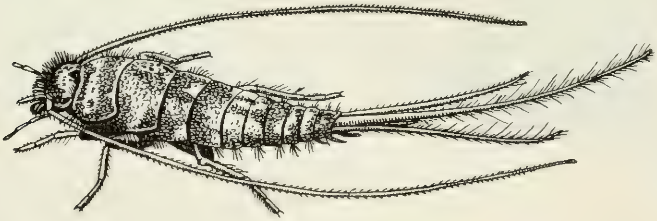


Fig. 15.26. Thysanura. A typical thysanuran, the firebrat, *Thermobia domestica.* (Redrawn, after Illinois Natural History Survey, from H. H. Ross, *A Textbook of Entomology*, second edition, copyright 1956 by John Wiley and Sons, Inc., printed by permission.)

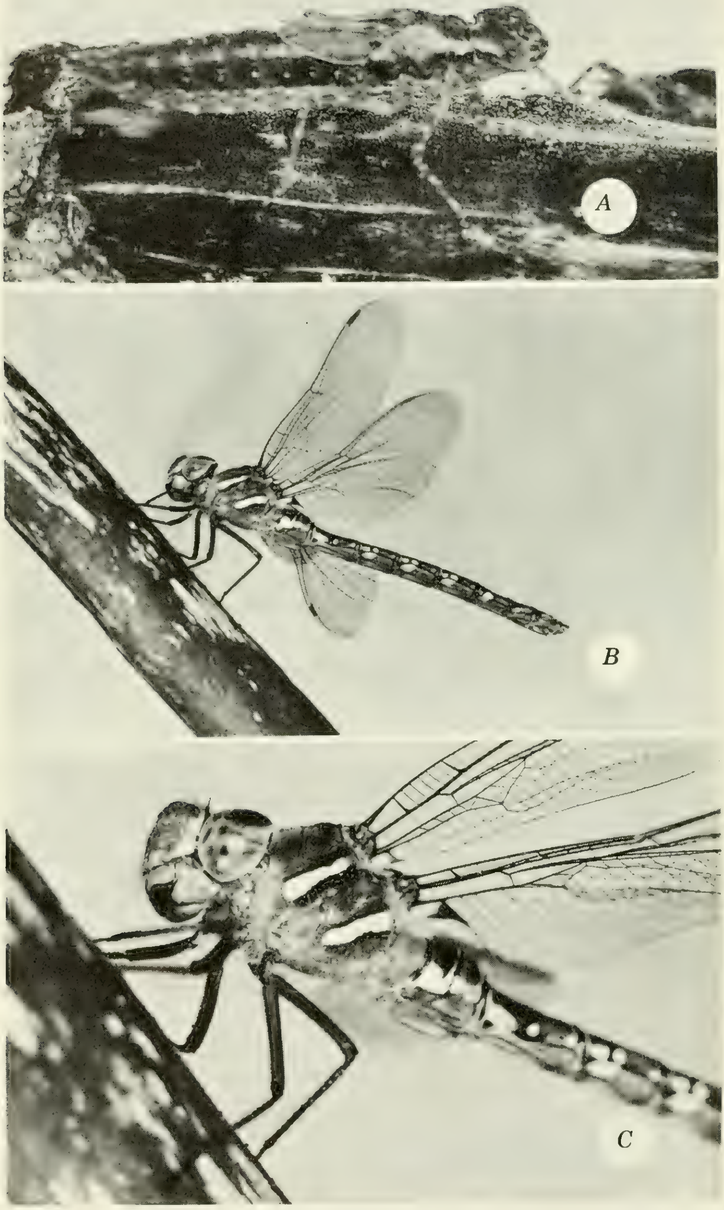


Fig. 15.27. Odonata. *A*, naiad of a dragonfly; in this immature stage the insect breathes by means of tracheal gills lining the rectum. *B* and *C*, two views of an adult dragonfly; note the large, many-faceted eyes, the stout mandibles, and the efficient wings. (Photographs by Charles Walcott.)

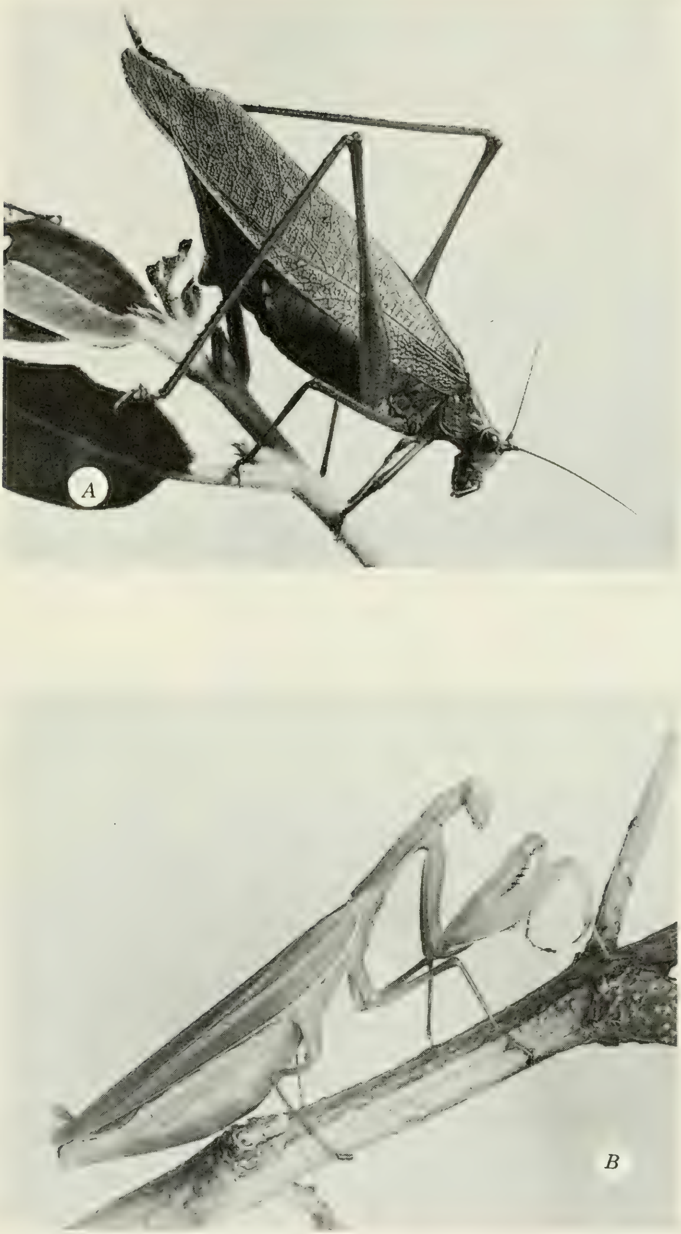


Fig. 15.28. Orthoptera. *A*, long-horned grasshopper, or katydid, *Scudderia furcata*. *B*, Chinese praying mantis, *Paratenodera sinensis*. Compare the modifications of the walking legs in these insects. (*A*, photograph by E. S. Ross; *B*, photograph by Charles Walcott.)

eyes of a dragonfly are unusually large, and this may be a factor in its efficiency as a predator of other flying insects. The clumsy naiads of dragonflies are found crawling along the bottom in fresh water; in these immature stages they are predators of small aquatic animals. Before the final molt to adulthood, they climb along the stem of a plant into the air, and after the adult emerges the cast skin of the naiad remains clinging to this support. Damsel flies, members of a different but related suborder, are smaller, more delicate of body and wing, and less efficient in flight. The life cycle, way of life, and general features are very similar to those of dragonflies.

Order Orthoptera (straight wings)—locusts and their relatives, grasshoppers, katydids, crickets, cockroaches, walking sticks, and praying mantises. In all of these, the mouth parts are mandibulate, and the life cycle is paurometabolous, with gradual metamorphosis. There are usually two pairs of wings, the anterior pair being modified to form thick, tough covers for the membranous posterior pair.

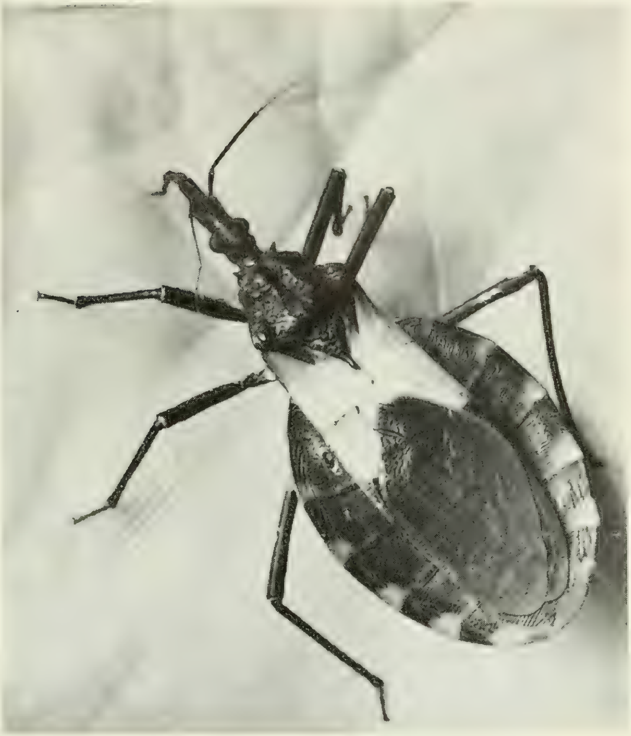
Crickets and katydids resemble locusts sufficiently in their general external features to be recognized at once as allied forms. The crickets that are most familiar are the house and field crickets of the genus *Gryllus*. The hind legs are elongated for jumping, as in the locust. In many species the wings are reduced in size, and some crickets are wingless. In connection with the nocturnal activities of these animals, the antennae, which are long and slender, are highly specialized as tactile organs. In males certain of the wing veins are modified for the production of sounds. The mole cricket is a type with strongly modified, shovel-like anterior legs which it uses in burrowing. Katydids (Fig. 15.28) are like green grasshoppers with very long antennae; the females bear conspicuous blade-like ovipositors.

Walking sticks and mantids are interesting, the former because of their striking mimicry of twigs, and the latter for their efficiency in destroying other insects. The "praying mantis" possesses strongly modified anterior legs which form a pair of deadly pincers; as it waits for its insect prey, the mantis holds these appendages in an attitude suggestive of the folded hands of a supplicant (Fig. 15.28). Like the dragonflies, these insects are wrongly maligned as harmful; they are actually so beneficial in their capacity of insect predators that mantises and their characteristic egg masses are protected by law in many parts of this country.

Order Hemiptera or Heteroptera (half-wings or different wings)—true bugs, the only insects that may properly be called "bugs." Representative examples are the cabbage bug, the squash bug, the assassin bug, and the water boatman. The mouth parts of these insects are suctorial; the wings overlap across the dorsal midline, and the anterior pair are thick at their bases and membranous at their tips. The life cycle in all hemipterans is paurometabolous.

The squash bug, *Anasa tristis*, which is a pest upon squash and pumpkin vines the country over, is perhaps best known by the disagreeable odor it emits when handled. It is representative of the true bugs with their mouth parts

Fig. 15.29. Hemiptera. A cone-nose bug, *Triatoma.* Note the extended mouth parts, modified for piercing and bloodsucking, and the characteristically half-membranous wings. (Photograph by E. S. Ross.)



adapted for piercing and sucking, and their wings showing the X-shaped pattern by which hemipterans are commonly recognized. The adults hibernate over the winter, dying in the spring soon after eggs have been laid upon the sprouts of vines where the young will feed. The nymphs, like those of the locust, are at first wingless individuals which undergo a series of molts before attaining adulthood. They feed by piercing the leaves and stems of the plant with their beak-like mouth parts and sucking the juices.

Most hemipterans appear to feed upon plant juices, but the members of some families are predators upon other insects. A few, like the assassin bugs, habitually attack vertebrates, piercing the skin and sucking blood (Fig. 15.29). This is the chief means of infection and spread of the affliction of man known as Chagas' disease, native to the American tropics. The causative organism is a blood-inhabiting flagellate protozoan, *Trypanosoma cruzi*, which multiplies in the gut of the insect host, very much like the parasite causing African sleeping sickness (p. 244).

Order Coleoptera (sheath wings)—widely distributed and highly varied insects known as beetles. The mouth parts are mandibulate but in the weevils, or snout beetles, form a piercing beak. The anterior pair of wings are modified as stout covers beneath which the posterior wings are folded in a complex manner. The life cycle of beetles is holometabolous.

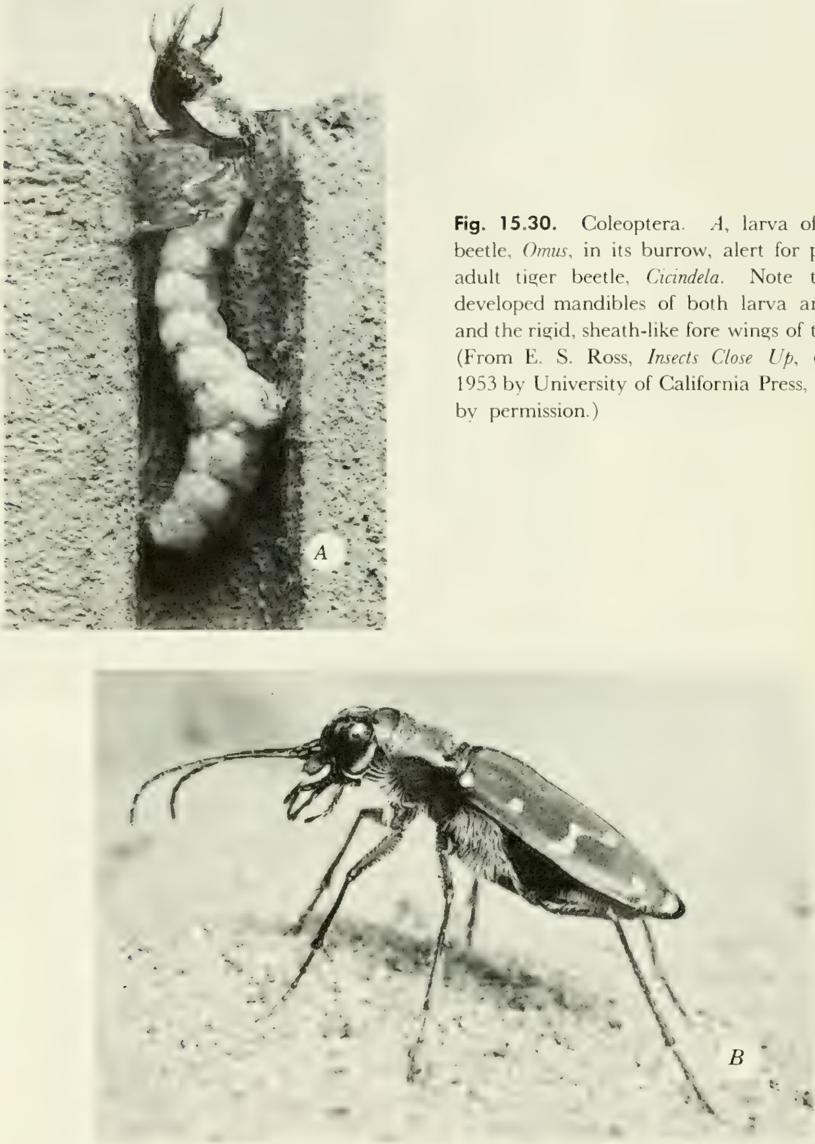


Fig. 15.30. Coleoptera. *A*, larva of a tiger beetle, *Omus*, in its burrow, alert for prey. *B*, adult tiger beetle, *Cicindela*. Note the well-developed mandibles of both larva and adult, and the rigid, sheath-like fore wings of the adult. (From E. S. Ross, *Insects Close Up*, copyright 1953 by University of California Press, reprinted by permission.)

The Colorado potato beetle, *Leptinotarsa decemlineata*, like other beetles, has fore wings specialized into a pair of covers, or **elytrae**, which fit together so tightly along the median line that they seem at first glance to form the dorsal side of a wingless body. When the elytrae are lifted, the functional hind wings are found folded beneath. In flight, the fore wings do not vibrate but are held stretched upward and outward in a V, to clear the rapidly beating hind wings. Eggs of the potato beetle are fastened to leaves of the potato plant; at the close of the embryonic period the humpbacked larvae, or grubs, emerge and begin their depredations by feeding on the vines. After a succession of larval stages, the mature grub crawls down from the plant and burrows into the soil before transforming into a pupa. The adult emerges after a week or 10 days and resumes the feeding interrupted by the pupal stage. The history of the potato beetle is interesting; the insect is native to western North America, where in its natural state it feeds upon purple nightshade, a wild species related to the potato. When potato culture was introduced into the Western states, the beetle transferred its activities to the potato plant and has since spread widely, by natural means, to practically every country where the potato is grown. Reservoir populations of potato beetles may always be found in stands of purple nightshade.

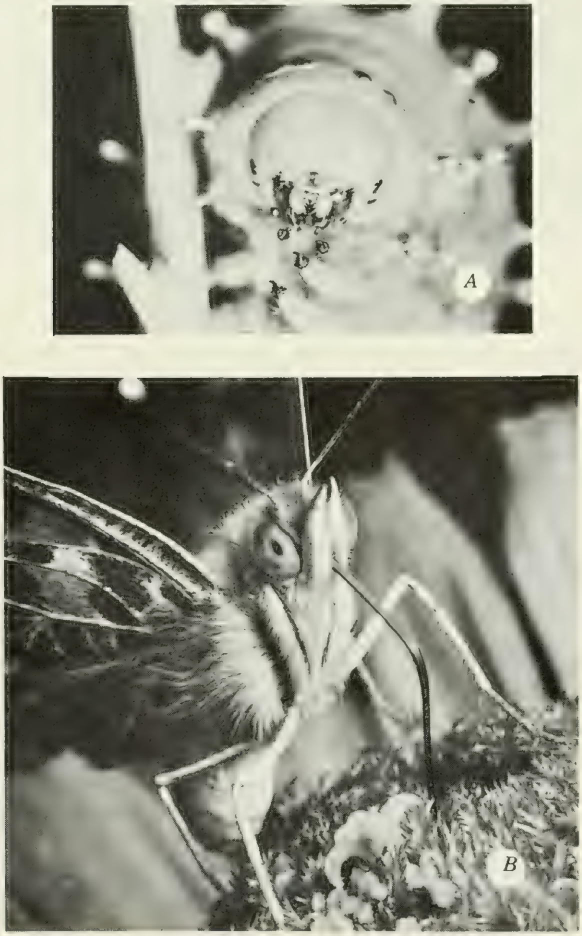
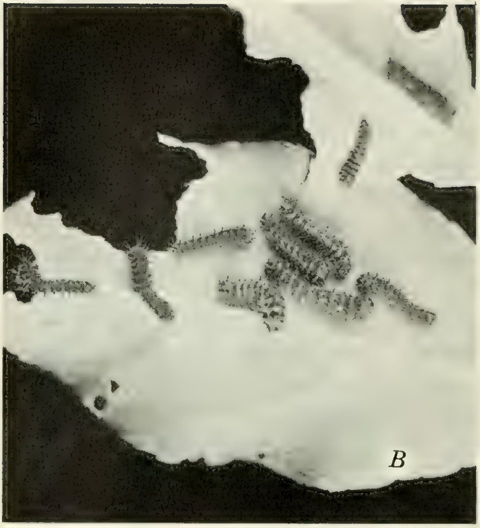


Fig. 15.31. Lepidoptera. Caterpillars usually possess mandibulate mouth parts like those of the moth larva shown in *A*. With metamorphosis, the mouth parts change to a suctorial type like those of the butterfly in *B*. This involves extreme modification of the maxillae in particular, which become lateral halves of a long tube, coiled at rest but capable of unrolling to reach the nectar in deep flowers. (*A*, photograph by Charles Walcott; *B*, photograph by E. S. Ross.)



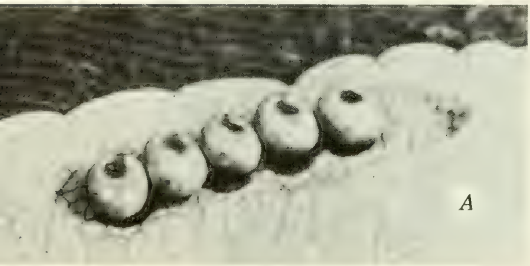
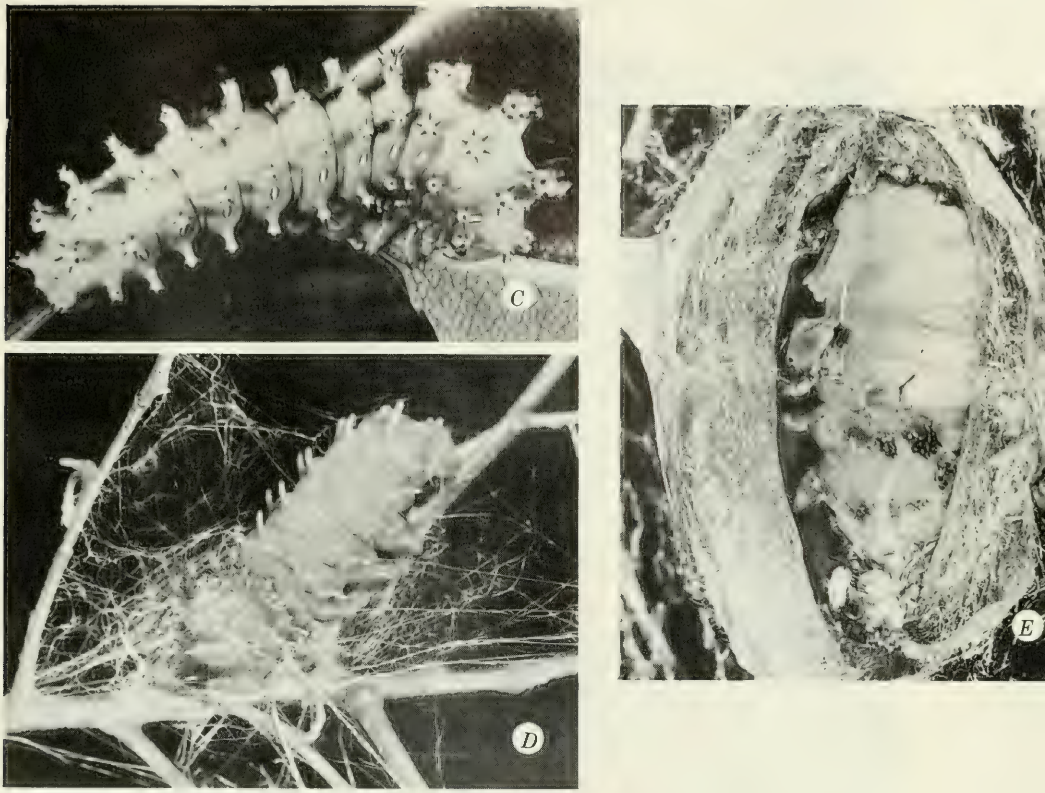


Fig. 15.32. Lepidoptera. Stages in the life cycle of a moth, *Platysamia cecropia*. *A*, group of eggs deposited on a wild-cherry leaf. *B*, young first-instar larvae feeding. *C*, young fourth-instar larva. *D*, mature (fifth-instar) larva beginning the construction of a cocoon. *E*, very early pupa within the cocoon, shedding the skin of the last larval stage. (Photographs by Charles Walcott.)

Taken as a group, beetles, like butterflies and moths, present a bewildering array of species adapted for many diverse conditions. Predaceous beetles inhabit ponds and streams in both larval and adult stages, and others, like the tiger beetles (Fig. 15.30), prey as larvae or adults on any small terrestrial animals they can capture. Many beetles bore into wood, particularly in their larval stages. The Japanese beetle, *Popillia japonica*, spends its larval life in the soil, feeding on grass roots and causing serious damage to turf grasses. The adult feeds voraciously on a wide variety of plants, including roses and fruit trees.

Order Lepidoptera (scale wings)—butterflies and moths. In this order, the mouth parts are either suctorial or non-functional in the adult stage but mandibulate in the larvae, which are called **caterpillars** (Fig. 15.31). There are two pairs of membranous wings in the adult, covered with minute, overlapping scales which are responsible for the color patterns. The life cycle is always holometabolous.

Among butterflies, the monarch or milkweed butterfly, *Danaus menippe* (=*Anosia plexippus*), is one of our commonest species. It ranges all over North and South America and occurs in other lands also, particularly western Europe, Australia, and the Pacific islands. Eggs of this insect are laid singly upon leaves of various milkweeds, and in a few days at summer temperatures



they hatch to produce minute larvae. The larvae feed on the leaves of the plant, molting several times as they increase in size during the 2 or 3 weeks of the larval period. Mature larvae are light-green caterpillars, conspicuously banded with black and yellow stripes, and with pairs of antenna-like projections toward each end. The molt marking the end of the larval period produces the so-called **chrysalis**, or pupa, in which such distinctive adult features as wings and antennae are recognizable. The adult emerges after 10 or 15 days, inflates its wings, and appears as the familiar flying form. In autumn the adults are killed by cold, or they migrate southward in great swarms to pass the winter in subtropical regions, returning to the north in spring. Other butterflies have different seasonal relationships, some passing the northern winter in the pupal stage, others as eggs that hatch in early spring.

Moths, of which there are very many species, are usually nocturnal in their activities, whereas butterflies are typically active during the daylight hours. Moths have feathery antennae and hold their wings horizontally at rest; butterflies have slender, clubbed antennae and hold their wings vertically. Again, the pupal stage of the butterfly is typically a naked chrysalis attached to some object by a single thread; the pupae of most moths are surrounded by **cocoons** of silk, spun during the last larval stage. At the close of the pupal period, the pupal skin is molted within the cocoon, and the adult forces its

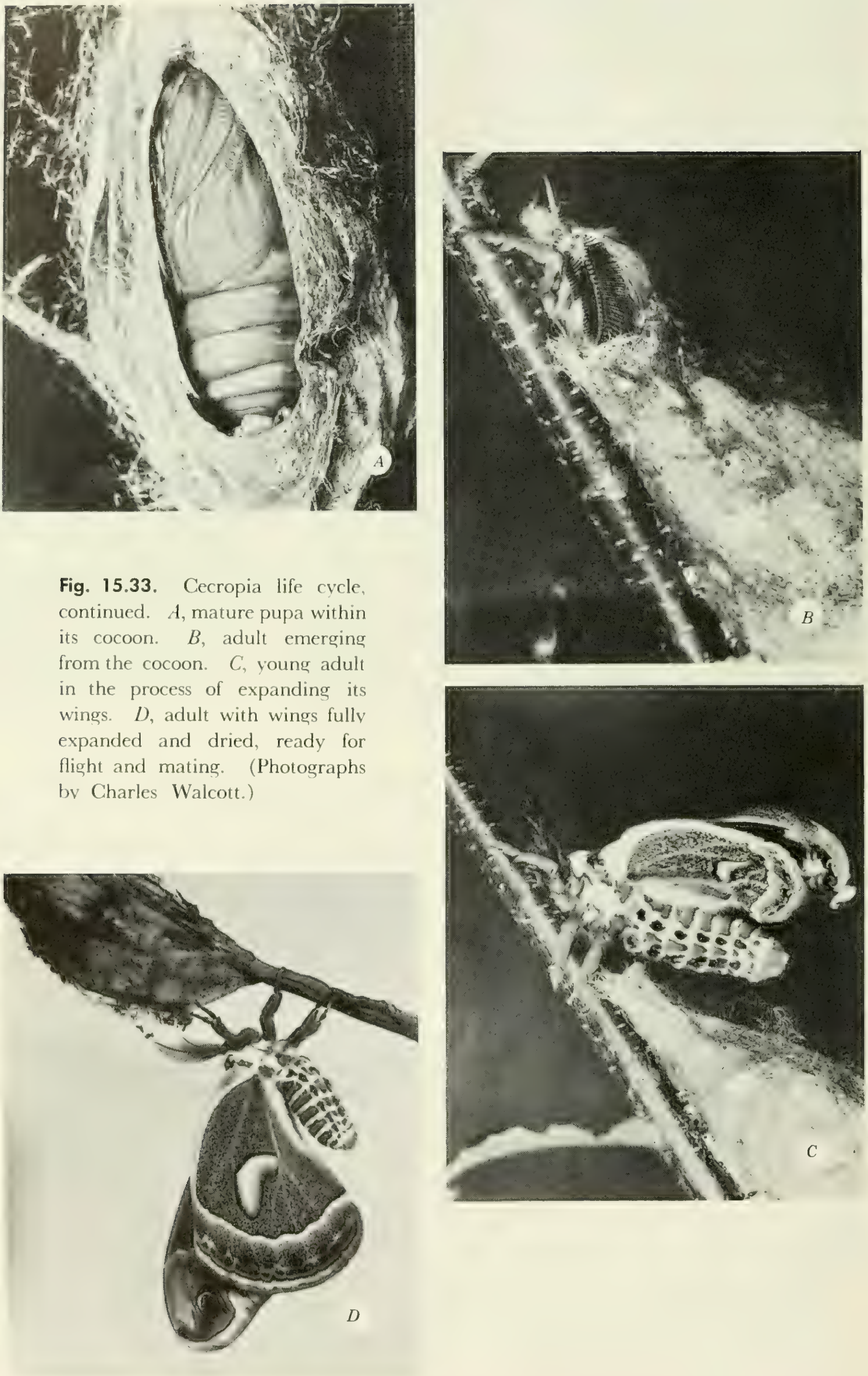


Fig. 15.33. Cecropia life cycle, continued. *A*, mature pupa within its cocoon. *B*, adult emerging from the cocoon. *C*, young adult in the process of expanding its wings. *D*, adult with wings fully expanded and dried, ready for flight and mating. (Photographs by Charles Walcott.)

way out of the cocoon to spread and dry its wings (Figs. 15.32, 15.33). The household pest known as the clothes moth (*Tineola bisselliella*) is a familiar example of this group; the silkworm, used in the Orient and in Europe for the commercial production of silk, is the larva of a large moth, *Bombyx mori*. Several species of giant silkworm moths are found in North America and, because of the large size of their larvae and pupae, have been very useful in studies on the biochemistry and endocrine control of metamorphosis.

Order Hymenoptera (membrane wings) -ants, bees, wasps, etc. The mouth parts are typically mandibulate but in the adult are often modified to form a tongue-like structure adapted for lapping liquids. The wings are membranous, and two pairs are usually present. The life cycle is holometabolous, with complete metamorphosis.

The Hymenoptera include a variety of types, ranging from insects of relatively simple habits to species with highly developed social organizations, such as honeybees and some ants. The examples that follow will illustrate this diversity.

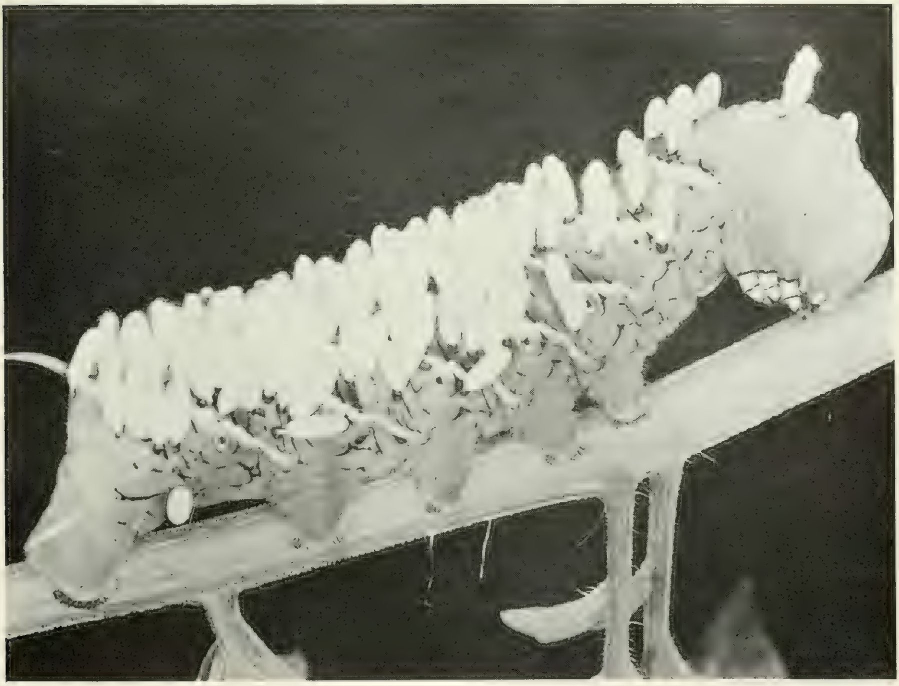


Fig. 15.34. Parasitism among insects. The large caterpillar (tomato hornworm) bears many cocoons of a small hymenopteran. An adult wasp deposited her eggs on the caterpillar, and the wasp larvae fed extensively on the tissues of the host before emerging to spin their cocoons and pupate. Such a parasitized caterpillar is incapable of completing its own life cycle; thus insects parasitizing other insects play an important role in the control of many agricultural pests. (Photograph by Charles Walcott.)

Parasitic hymenopterans include many species which pass their developmental stages as parasites within the bodies of other insects. Among these parasitic forms are **ichneumon wasps** and **braconid wasps** (Fig. 15.34), which usually deposit their eggs upon or within the bodies of a variety of other insects. After the larvae hatch, they live parasitically in the body of the host until their time of pupation; they then come to the surface and spin cocoons from which adult wasps later emerge. Caterpillars are often found covered with the minute cocoons of these parasites. Many times, an apparently normal cocoon of one of the giant silkworm moths will be found to contain not the pupa of the moth but that of an ichneumon wasp, whose larva has completely devoured the caterpillar which spun the cocoon. The activities of such parasitic wasps have sometimes helped check outbreaks or invasions of insect pests of economic importance.

Non-parasitic wasps may be subdivided into solitary forms, in which there is no colonial organization, and social wasps, which live in colonies like those of bees and ants. Mud daubers of the genus *Sceliphron* are solitary wasps that build a nest of mud fashioned into several tubes. When one of these tubes is completed, the wasp collects small spiders, which she paralyzes with her sting and with which she fills the tube. She then deposits a single egg in the outer end of the tube before sealing it with mud. When the larva hatches, it uses the spiders as food, eventually pupating and finally emerging as a winged adult, which gnaws its way out of the tube. Only females are active in the nest-building operation; males apparently die soon after mating. Digger wasps, excavating subterranean burrows which they provision with paralyzed insects, offer another example of hunting and food-storing activities (Fig. 15.35).

Among social wasps, species of the genus *Polistes* represent a simple type of social organization. They build nests of paper, which they make by chewing wood fibers and mixing them with saliva. A female *Polistes*, after hibernating through the winter, begins to construct a nest which by the end of the summer may reach a diameter of a foot or more. The nest is a plate-like group of individual paper-walled cylinders, generally fastened to some support by a slender stalk. The single female, or **queen**, which begins the construction, is soon aided in tending the young and adding to the nest by other females, the infertile **workers**, which hatch from her eggs. The males are **drones**, which do not work and which die soon after mating. The nests of hornets that hang from the limbs of trees are composed of a series of paper combs essentially like those of *Polistes* but enclosed in a common covering.

Among **bees** there are both solitary and social species and others that show transitional stages. Thus, it is possible to establish theoretically the steps through which the highly organized honeybee colony may have evolved. In solitary species each female constructs her own separate nest, in which an egg is laid and where food is either stored or brought to the larva during its development. Some of these solitary species show a tendency toward gregariousness, suggesting the beginnings of social life. They build many nests

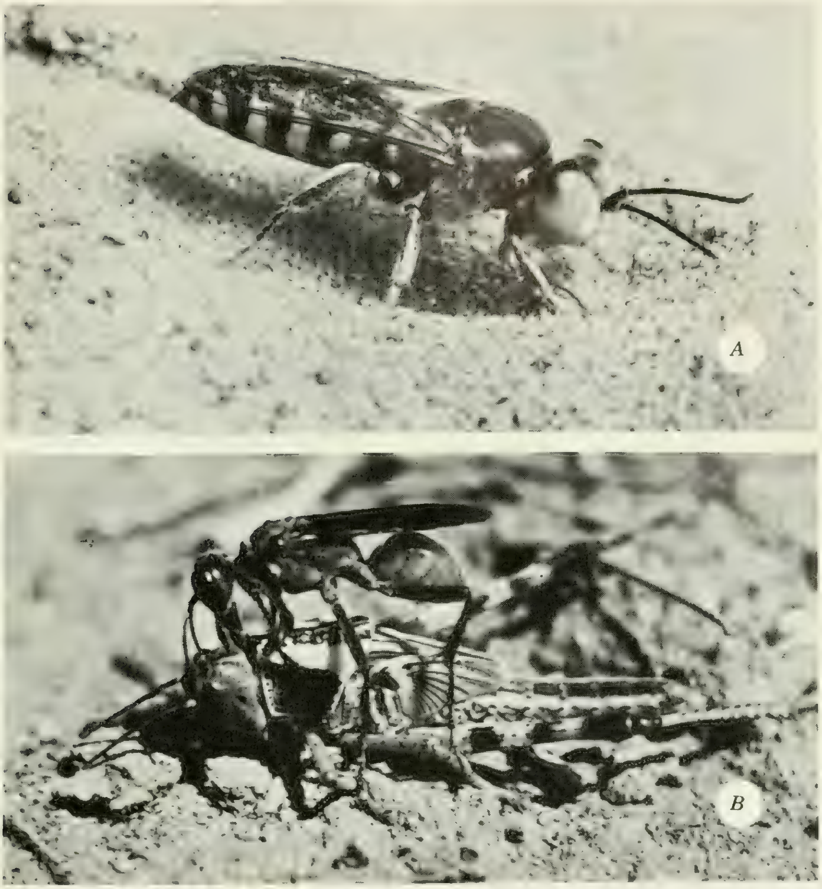


Fig. 15.35. Hymenoptera. *A*, a digger wasp, *Bembex*, beginning excavation of a burrow. *B*, a hunting wasp, *Chlorion*, preparing to transport a paralyzed nymphal locust to her burrow. There she will deposit an egg upon her living but helpless prey, and the larval wasp which hatches will feed upon the locust. By seeking various kinds of insects and spiders with which to provision their burrows, the hunting wasps are a significant factor in insect control. (From E. S. Ross, *Insects Close Up*, copyright 1953 by University of California Press, reprinted by permission.)

close together, although each nest belongs to a single individual. In others the nests are separate, but the neighbors cooperate in the construction of a common entrance. **Bumblebees** represent a more specialized organization, in which the females have become differentiated as fertile queens and infertile workers, and the males as drones; this is the usual situation among the social hymenopterans.

A colony of **honeybees** may be regarded as a further development of such a colonial organization as that of bumblebees. The honeybee workers keep the hive in repair, collect nectar and pollen and modify these substances for storage as honey and beebread, tend and feed the young, care for the queen, and are in general responsible for the maintenance of the organization. The queen, having once been inseminated, produces zygotes from which develop all the individuals of the colony. The males, or drones, develop from unfertilized, haploid eggs through parthenogenesis. The fertilized eggs produce larvae which are always females but which may develop into either sterile workers or fertile young queens, depending on the diet with which they are fed. Future queens are fed throughout larval life on "royal jelly," which permits full development of their genital organs. Other female larvae receive this diet only for a day or two; their genital organs fail to develop, and such physiologically castrate females become workers. There is some evidence indicating that workers in a colony obtain some secretion from their queen which generally suppresses the production of additional queens (cf. caste production in termites, pp. 458–459). The integrity of a colony with its single queen is thus maintained until the swarming period, when many workers leave the colony with the old queen, to found a new colony and build a new hive. When this happens, a part of the old colony is left behind to rear a new queen. The behavior of the individuals is a marvel of precision and seeming adaptation of means to ends, although it consists of reactions based on inherited reflexes, or instincts, which are modifiable only within very narrow limits. In addition to these innate complex behavior patterns, other phenomena of the life of the bee are of interest and remain to be accounted for. For example, how is it possible to explain the origin and inheritance of the highly specialized structural modifications of the workers? The legs of these insects bear specifically developed combs, pollen baskets, antenna cleaners, and so on, perfectly adapted to the food-gathering and other functions of the workers (Fig. 15.36); yet the workers are sterile and never produce offspring which could inherit these traits, and the queen and the drone, which are the parents of the workers, bear none of these specialized structures. The factors operating within the body of the queen, which evoke the production of either fertilized eggs or parthenogenetic eggs, and thus either female or male progeny, are also unaccounted for.

Only within recent years has some insight been gained into the means of communication between bees in a colony. Foraging scouts, when they have located a source of food, return to the hive and transmit to other workers information about the kind of food available, its abundance, and the distance and direction from the hive to the food supply. The kind of food, that is, generally the kind of flower from which it may be obtained, is communicated by both olfaction and taste. Other workers gather about the returning scout and "smell" with their antennae the characteristic fragrance of the flowers which clings to its body; similar information is transmitted with the nectar which the scout regurgitates from its honey stomach and which other workers ingest. Bees are capable of distinguishing large numbers of fragrant essential oils from flowers; they are confused by some which also smell alike to man. The distance-and-direction information is transmitted by a series of "dances"

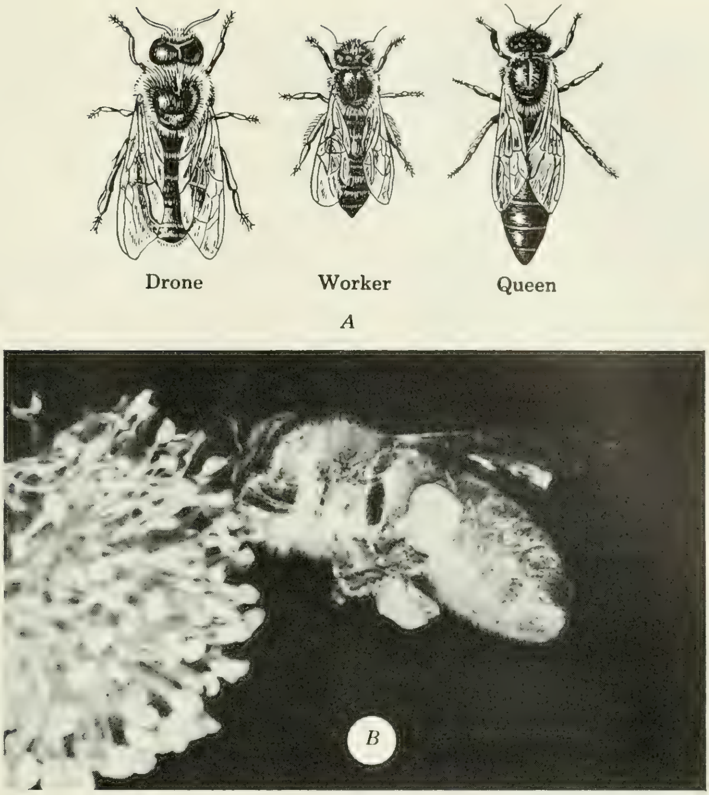
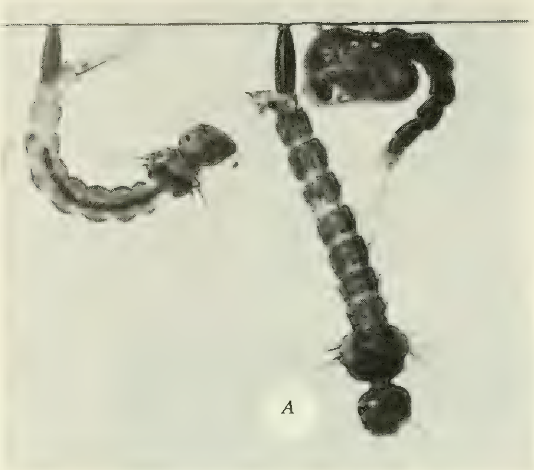
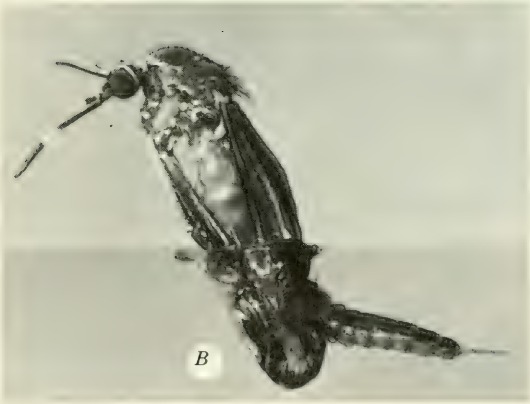


Fig. 15.36. Hymenoptera: the honeybee, *Apis mellifera*. *A*, comparative aspects of the three castes of a honeybee colony. *B*, a worker honeybee visiting a flower; note the bulging pollen baskets on the metathoracic legs of the insect, packed with pollen to be carried to the hive. These pollen baskets, along with other special modifications, are found only in the worker caste. (*A*, redrawn from K. von Frisch, 1953, *Biologie*, vol. 2, printed by permission of Bayerischer Schulbuch-Verlag; *B*, photograph by Charles Walcott.)

performed at the entrance of the hive by the returning forager; the dances are soon joined and imitated by other workers. A so-called "round dance" is performed when the food is near the hive, and the abundance of the supply is indicated by the vigor of the dance. For sources many hundreds of yards, or even a mile or more, from the hive, the forager performs a more complicated "waggle dance" involving a straight passage which indicates the compass direction to be flown in seeking the food. By imitating the straight part of the dance, other workers evidently perceive the pattern of polarization of light from the sky, which is characteristic of the compass heading they must fly. Analysis and integration of polarized light are presumably functions of the well-developed compound eyes of these insects. Fantastic as these statements may seem, they are all based on sound experimental evidence gathered





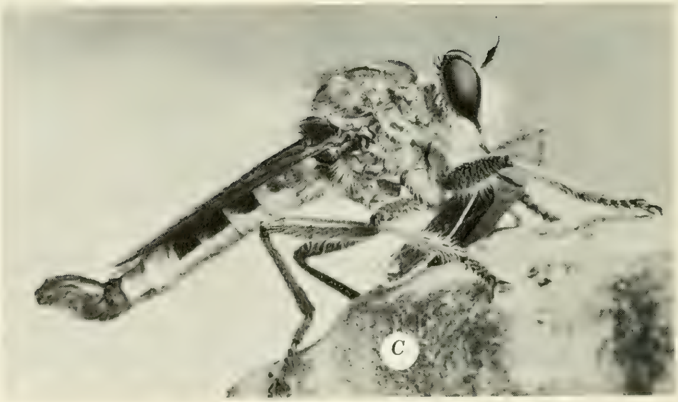


Fig. 15.37. Diptera. *A*, larvae and pupa of a mosquito, *Aëdes*, breathing at the surface of the water; the functional spiracles of the larva are posterior, whereas those of the pupa open dorsally on the thorax. *B*, emergence of an adult *Aëdes* from its pupal skin. *C*, a predaceous robber fly, *Apiocera*, feeding upon the juices of a leafhopper. Note the small, club-shaped haltere, or balancer, attached to the metathorax of the fly; this is the characteristic condition of the hind wings in dipterans. (From E. S. Ross, *Insects Close Up*, copyright 1953 by University of California Press, reprinted by permission.)

for the most part by the eminent Austrian biologist Karl von Frisch and since confirmed by many other experimenters.[1]

Ants appear even more specialized in their social life than other hymenopterans, since there are no existing examples of solitary ants, and since the workers of most ant colonies are specialized into two or more castes which carry on special activities. Ant colonies, particularly in some of the tropical species, may be very large, as judged both from the size of the nest and from the number of individual members. The essential features of social organization are illustrated by many of our native forms. In a typical example, the males, which are winged throughout their brief existence, participate in the mating flight with the females and then die. These females, the queens, then pull off their wings, establish nests, lay eggs, and tend the young until workers develop to carry on these labors. When the mating season approaches, winged males and females are produced and leave the nests in the swarms that are seen at certain seasons of the year.

Ants, bees, and wasps among the Hymenoptera, as well as termites (order Isoptera, p. 458), are of particular interest because of their social life and their behavior. From the standpoint of social organization, insects represent the only group in which anything approaching the complexity of human society exists. From the standpoint of animal behavior, these insects exhibit amazing instinctive reactions, the result of inherited reflexes so fixed in their nature that they have become recognizable characteristics of the species, just as reliable as any morphological characteristics.

Order Diptera (two wings)—true flies, such as the housefly and the mosquito. The mouth parts of the dipterans are typically suctorial, although they have been modified in various ways, as for lapping and for piercing and sucking. There is an anterior pair of membranous, functional wings; the posterior wings are much reduced to form club-shaped **halteres** or balancers (Fig. 15.37), which vibrate in flight and have been demonstrated to serve as gyroscopic stabilizers. The life cycle is holometabolous, with larvae commonly known as maggots.

The common housefly, *Musca domestica*, is perhaps the most familiar of all insects; and, since it is recognized as a carrier of disease-producing microorganisms, its life cycle is widely known. The adult has mouth parts adapted for lapping fluids; in feeding, it generally extrudes saliva onto the food and then ingests the saliva with dissolved food substances. The fly feeds upon almost any kind of organic matter that may be available. The extent to which houseflies may become distributors of bacteria can be shown by allowing a single individual to crawl across a sterile plate of nutrient gelatin and noting the colonies of bacteria which later appear along its trail. Eggs are laid in various kinds of decomposing organic matter. Larvae, or maggots, hatch in about 6 hours and grow through three larval instars, lasting a total of 5 or 6 days, before pupation. The pupal case, or **puparium**, is formed by the hardened and darkened exoskeleton of the last-stage larva. The adult emerges from this case about 5 days after pupation. Thus, a generation may be developed every 12 days under favorable conditions; and, since every female may lay about 100 eggs, the potential rate of multiplication in a single season is very great. Many of the adults die with the onset of winter, but some hibernate in protected places. These overwintering individuals then become active again in early spring and lay the eggs from which the flies of another season arise.

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[1] For a fuller and entirely delightful account of these and other interesting phenomena among honeybees, see Karl von Frisch, *Bees: their Vision, Chemical Senses, and Language*, copyright 1950 by Cornell University Press.

Mosquitoes have assumed great importance since it was discovered, about 1895, that certain mosquitoes carry the protozoan parasite causing malaria, and later, that the virus causing yellow fever is also transmitted by mosquitoes. Adult females, whose mouth parts are capable of piercing the skin and sucking the blood of man, are responsible for the transfer of these parasites, since the mouth parts of the male cannot penetrate the human skin. Apparently the malaria parasites of importance in human malaria are carried only by mosquitoes of the genus *Anopheles*, and the virus of yellow fever is carried only by members of the genus *Aëdes*. The most common mosquitoes of temperate latitudes belong to the genus *Culex*, which does not serve as a host for either of these parasites. Culicine mosquitoes lay eggs fastened together in little rafts which float upon the surface of fresh waters. The larvae hatching from these eggs are the **wrigglers** commonly seen in standing water, where they hang suspended from the surface film by tubes at the posterior ends of their bodies; air reaches their tracheae through these tubes (Fig. 15.37). The larval stage of *Culex* lasts from 1 to 4 weeks, depending on the species and to some extent on temperature and the abundance of the food supply. The food during this period consists of minute organisms captured and ingested by the mandibulate mouth parts of the larva. With their third molt the larvae change into active but non-feeding pupae, in which the head and thoracic regions are enlarged and the wings and antennae of the adult can be seen, as in the chrysalis of a butterfly. These pupae, like the larvae, must secure air from the surface, but the air tubes of the pupa are located on the dorsal side of the thorax. After 2 to 5 days the pupal skin is shed, and the adult emerges (Fig. 15.37). Both larvae and pupae are killed when the water in which they live is covered with a film of oil, for this film prevents their access to the atmospheric air which they require. Other methods of control involve drainage of swamps and other bodies of stagnant water, and emptying even such smaller breeding places as tin cans and rain barrels.

A great many insects of economic, medical, and veterinary importance to man belong to the order Diptera. The tsetse fly of Africa, which transmits the trypanosomes of sleeping sickness; stable flies, horn flies, botflies, warble flies, horseflies, and screwworm flies which variously parasitize, feed upon, or otherwise annoy cattle and horses; the Hessian fly, which destroys standing crops of grain; all these are but a few of the insects with which man must constantly contend.

Importance of Insects to Man. Although a few insects, such as the silkworm and the honeybee, are specifically useful, a vast array of insect species are detrimental to man. Again, some insects have important roles in the economy of nature, in the pollination of flowers, as food for many animals, and as destroyers of other insects harmful to livestock and crops. More often, however, the insect is destructive of the plant and animal life most necessary to man. Estimates made for the United States in recent years place the total insect damage to crops, domestic animals, and stored products at millions of dollars annually. In the past man had to reckon more with his fellow mammals; in the present and for the future the insects, above all other forms of life, strive with man for the control of his environment. Finally, many insects are dangerous to man as pests of his body and his habitations and, most important of all, as hosts and carriers of the microorganisms of various diseases of humans.

With increasing knowledge of habits, life cycles, and ecological relationships of economically important insects, it has become possible to institute various measures for their control or eradication. Natural factors of insect control, such as bacterial and parasitic diseases affecting insects themselves, have been advantageous. Mechanical methods of picking the pests from plants and destroying them, as well as cutting and burning infested plants, are of considerable value.

The most widespread technique of insect control is by means of chemicals. These are sometimes used to repel insects or to attract them to poisoned food and into traps; but most commonly they are employed as **insecticides**. Arsenic, sulfur, and fluorine compounds are among the oldest and most common insect poisons, along with a variety of soaps, oils, nicotine compounds, and an increasing number of very effective synthetic organic products. Among these last is DDT (dichloro diphenyl trichloroethane) made famous by its extensive use in World War II. Many ingenious devices have been developed for the application of these insecticides to growing plants. One of the most effective is the use of airplanes and helicopters to spray or dust crops and woodlands on a large scale, or to reach areas not easily accessible by other means.

Insecticides exert their effects on insects in a variety of ways, notably as "stomach poisons" when ingested with food, as in the case of arsenic compounds, or as contact agents by clogging the spiracles or tracheal tubes, as oil sprays do. The action of DDT and some of the newer organic insecticides is somewhat different: DDT has been shown to operate as a nerve poison, blocking the action of a specific enzyme which normally inhibits constant excitation along nerve pathways. Under the influence of DDT, a susceptible organism is thrown into violent and continuous muscular spasms which end with the death of the animal. Not all insect species of economic importance are susceptible to DDT, however; and of those which are, some populations rapidly develop strains that are markedly resistant to concentrations of the poison ordinarily fatal to the species. In the same manner, populations of scale insects have developed in California which are resistant to the fatal effects of one of the most potent poisons known to man, hydrocyanic acid gas. These are examples of the general adaptability of living organisms to environmental changes and may be regarded as the result of a process of **artificial selection.** According to this interpretation, certain individuals, by the chance operation of random mutations, are capable of withstanding ordinarily lethal concentrations of the poison. Continued subjection to the insecticide rigorously "selects" for survival those individuals which are most resistant, until eventually the breeding population is composed entirely, or preponderantly, of resistant stocks.

THE CLASSES CHILOPODA AND DIPLOPODA

Members of these two arthropod classes show certain superficial similarities: they are tracheate animals with mandibulate mouth parts, with long, slender bodies composed of a large but indefinite number of segments, and with numerous paired, jointed appendages. These similarities have led to their classification within a single group, the class **Myriapoda,** in older systems. However, closer study reveals many significant differences between centipedes and millipedes which indicate a more remote relationship.

Centipedes are somewhat flattened dorsoventrally; the body is composed of a definite **head**—bearing **antennae, ocelli,** and the **mouth parts**—and a many-segmented **trunk** (Fig. 15.38). Each of the trunk segments, except the last two, bears a pair of walking legs; those of the first segment are modified into conspicuous **poison fangs,** sometimes referred to as **maxillipeds.** The gonads are dorsal to the gut, and, as in insects, the genital openings are at the posterior end of the body. Centipedes are predatory carnivores, feeding on small animals captured and killed with the aid of the poison fangs.

Millipedes are cylindrical and worm-like. As in centipedes, a head is present, bearing antennae and groups of ocelli. The trunk, however, may be divided into four anterior **thoracic** segments and a large number of **abdominal** segments. Those of the abdominal region are fused in pairs, so that each apparent division seems to bear two pairs of walking legs (Fig. 15.38). The gonads lie ventral to the gut, and the genital openings are anterior, on one of the thoracic segments. Millipedes are retiring, herbivorous animals which when disturbed usually roll up into a tight spiral and emit a disagreeable odor from segmental scent glands.

Diplopods, and some chilopods, are characterized by **anamorphic growth:** the young individual does not have the full adult number of somites, but at each molt as it grows to maturity new segments are added in a posterior zone of growth, just anterior to the segment bearing the anus. As we have seen, this type of growth is characteristic of annelids, as well as of the most primitive insects (Protura). Other features reminiscent of annelids are the long, worm-like body, the relatively undifferentiated nature of the somites, and the presence of paired appendages on most of the segments. More advanced characteristics include the development of a definite head with specific

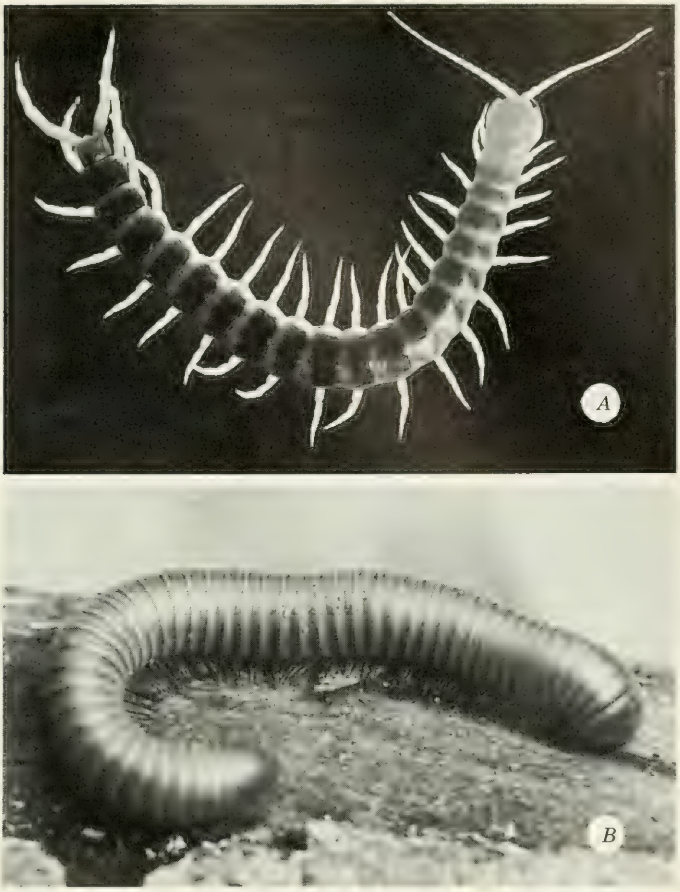

Fig. 15.38. *A*, Chilopoda: a large tropical centipede. Note the poison fangs attached to the posterior end of the head; each contains in its base a gland, the toxic secretion of which passes through a duct to a minute pore near the tip of the fang. *B*, Diplopoda: a millipede, *Spirobolus*. There are two pairs of appendages for each division of the body, with the exception of a few just behind the head. Each division represents the product of fusion between two adjacent somites. (*A*, photograph courtesy New York Zoological Society; *B*, photograph by Charles W. Schwartz.)

mouth parts and sense organs, the tracheal respiratory system with segmental spiracles, and the exoskeleton which must be molted to permit growth. Altogether, chilopods and diplopods present an interesting mixture of annelid-like and insect-like features, in addition to adaptive characteristics peculiar to their kinds. This has led to the supposition that their ancestors developed from an evolutionary stock of terrestrial mandibulate arthropods rather early in its history, and that they demonstrate the capacity of this stock to evolve features which were later perfected in the Insecta.

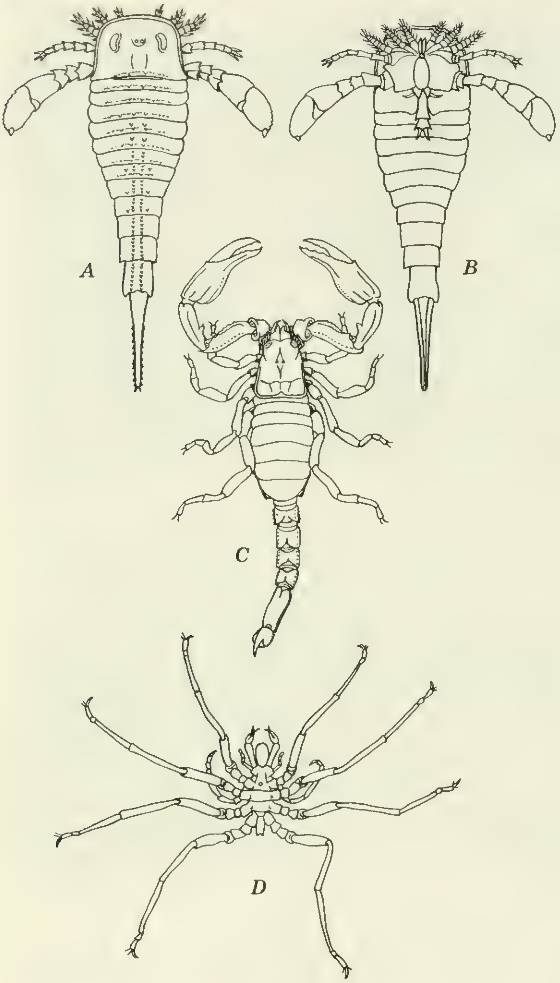

Fig. 15.39. Representative Chelicerata. *A* and *B*, class Eurypterida: restoration of a generalized fossil eurypterid, dorsal and ventral views. *C*, class Arachnida: a scorpion, *Chactas*. *D*, class Pycnogonida: a sea spider, *Nymphon*. (Redrawn from R. E. Snodgrass, *Textbook of Arthropod Anatomy*, copyright 1952 by Cornell University Press, printed by permission.)

THE SUBPHYLUM CHELICERATA

In addition to the extinct eurypterids, chelicerates include horseshoe crabs, pycnogonids, and arachnids (Fig. 15.39); within this last group are placed such familiar forms as spiders, scorpions, ticks, and mites. In all chelicerates the body is divided into an anterior **prosoma** and a posterior **opisthosoma**; these regions are comparable, but not equivalent, to the cephalothorax and abdomen of crustaceans. One of the major unifying features of chelicerates is their possession of six pairs of appendages, borne on the prosoma and developed in a consistent pattern. The anteriormost of these are the pincer-like **chelicerae**, from which the name of the group is derived. The second pair, the so-called **pedipalps**, are variously specialized: in the horseshoe

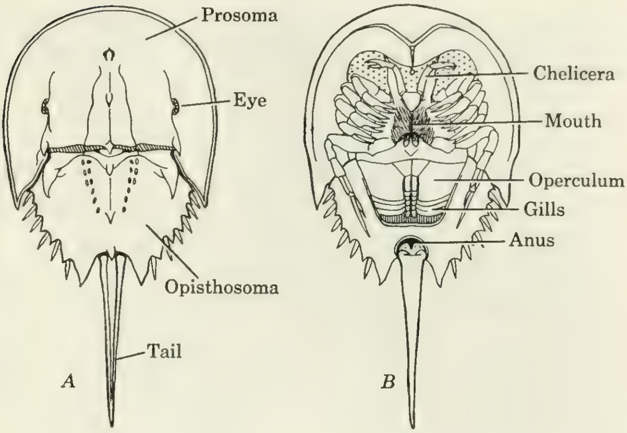

Fig. 15.40. Class Xiphosurida: *Limulus polyphemus*, the horseshoe crab of the Atlantic coast of North America. (Redrawn from R. E. Snodgrass, *Textbook of Arthropod Anatomy*, copyright 1952 by Cornell University Press, printed by permission.)

crab they are unmodified walking legs; in scorpions they form the conspicuous great chelae used in capturing prey; in male spiders they are often very complex structures adapted for the transfer of spermatozoa to the female at mating. The remaining four pairs of appendages are relatively undifferentiated walking legs. Only the horseshoe crab, *Limulus*, exceptional in many respects, bears segmental appendages on the opisthosoma (Fig. 15.40).

Most modern chelicerates are small, terrestrial animals. *Limulus* is an exception to this generalization also; it is a marine form, often reaching 2 feet in length. Fossil remains of forms ancestral to *Limulus* show that this genus has remained almost unchanged since Devonian times, some 350,000,000 years ago. In correlation with its marine habitat, *Limulus* bears on the ventral side of the opisthosoma many leaf-like gills which function in oxygenation of the blood. These delicate gills are protected by plate-like expansions of the opisthosomatic appendages, used also for swimming. Among terrestrial arachnids, scorpions and most spiders have developed internal cavities termed **book lungs**, containing many thin, hollow plates between which the blood

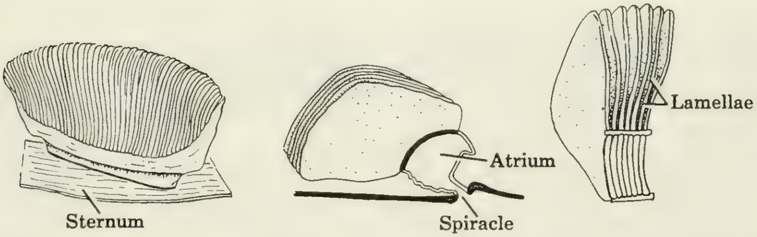

Fig. 15.41. Book lung of a scorpion. The hollow lamellae, filled with air, communicate with the cavity of the atrium; blood circulates between the individual lamellae. (Redrawn from R. E. Snodgrass, *Textbook of Arthropod Anatomy*, copyright 1952 by Cornell University Press, printed by permission.)

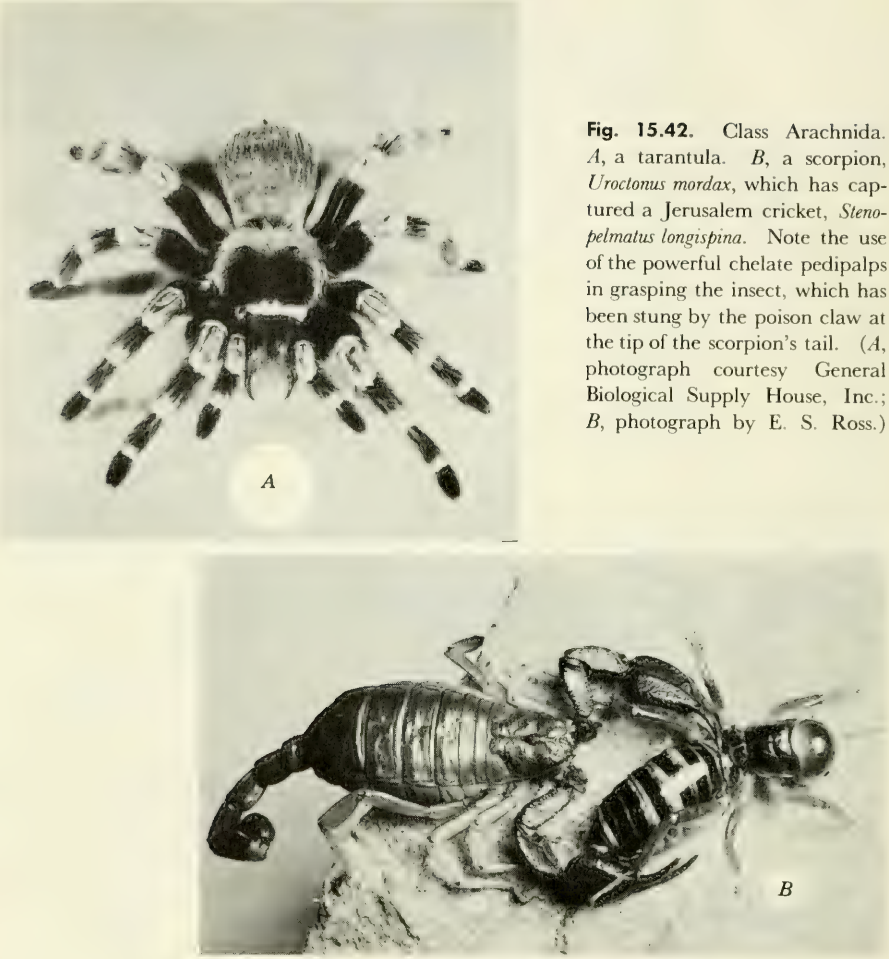

Fig. 15.42. Class Arachnida. *A*, a tarantula. *B*, a scorpion, *Uroctonus mordax*, which has captured a Jerusalem cricket, *Stenopelmatus longispina*. Note the use of the powerful chelate pedipalps in grasping the insect, which has been stung by the poison claw at the tip of the scorpion's tail. (*A*, photograph courtesy General Biological Supply House, Inc.; *B*, photograph by E. S. Ross.)

circulates (Fig. 15.41). The individual "pages" of the book lung contain air spaces, and the collective air spaces of each lung communicate with the outside through a slit-like spiracular opening. Some spiders possess, in addition to or in place of book lungs, tracheal systems analogous to those of insects, with segmentally arranged spiracles

Relatively few spiders, among them the "black widow," *Latrodectes mactans*, are dangerous to man. By far the majority of spiders are beneficial through their destruction of insects (Fig. 15.42). Of even greater economic importance are the arachnids called ticks and mites, many of which are parasitic on man and his domestic animals, and a few of which transmit disease-producing microorganisms from host to host.

The Phylum Onychophora

The onychophores ("claw bearers"), sometimes considered a class of the phylum Arthropoda, are a small but interesting group of animals represented in the modern fauna by only about a dozen genera. Of these, the genus *Peripatus* is best known. This "walking worm" is a predaceous animal, feeding upon small insects; it is restricted to moist terrestrial habitats in subtropical regions. *Peripatus* presents a curious mixture of characteristics, some reminiscent of annelids and others resembling those of arthropods. The body is worm-like, with numerous pairs of appendages arising at intervals (Fig. 15.43). Unlike those of arthropods, these appendages are not jointed but are fleshy, lobe-like outgrowths of the body wall containing groups of muscles and bearing hooked claws at their distal ends. The head consists of a simple cephalic lobe bearing antennae, simple eyes, and a mandibulate mouth. The body of the adult is not segmented, although many structures lie in what appears to be a segmental arrangement. In embryonic development a series of paired coelomic pouches form, but the body cavity of the adult is a hemocoel; remnants of the coelom are found only in the cavities of the gonads and of the excretory organs. These organs are a series of paired nephridia, closed internally by reduced coelomic end sacs and opening externally at pores on the bases of the legs. The nephridial tubules are ciliated like those of annelids; cilia are altogether lacking in all arthropods. The body wall of *Peripatus* is covered by a thin, flexible cuticle rather than a hardened exoskeleton. Although a tracheal system is present as in many arthropods, in onychophores the tracheae arise in tufts from the inner ends of spiracular openings which are scattered over the surface of the body, not restricted to segmental intervals.

Taken as a group, onychophores may be considered as persistent, little-changed representatives of an ancient stock of animals which evolved from the annelid-arthropod stem independently of the groups that later gave rise to

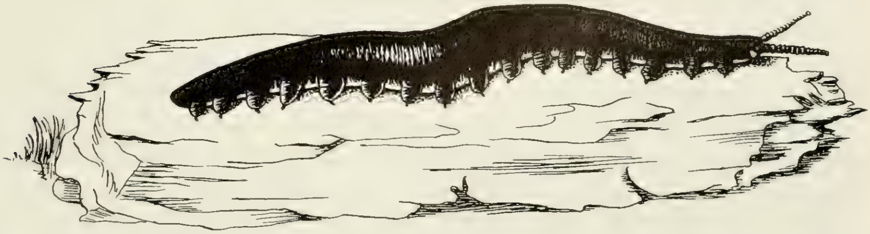

Fig. 15.43. Phylum Onychophora: general features of *Peripatus capensis*, natural size. Note the serially repeated, lobe-like, clawed appendages of the trunk, which are characteristic of animals in this phylum. (Redrawn from A. Sedgwick, 1888, *Studies from the Morphological Laboratory in the University of Cambridge*, vol. 4.)

true arthropods. Fossil remains that are unmistakably onychophoran are known from the middle Cambrian period, and the external features of *Peripatus* show remarkably few alterations when compared with those of the ancient forms. *Peripatus* should not be regarded as a "missing link" between annelids and insects (cf. p. 630). *Peripatus* itself and onychophores generally are in their own way highly specialized evolutionary end forms, and such end forms cannot logically be considered as links between different phyla. In addition, it would be surprising indeed if insects, the most advanced class of modern arthropods, could be traced directly to annelid-like ancestors.

The Arthropod Body Plan and Its Evolution

The fundamental similarities in general organization between annelids and the arthropod-onychophore groups indicate that a common ancestry lies behind all these types. If we look for factors significant in determining the different evolutionary directions taken by annelids and arthropods, leading to the marked differences between their modern representatives, one factor stands out pre-eminently—the development of the hardened exoskeleton in the arthropod stem. We may assume that somewhere in the evolutionary history of arthropods, after the divergence of the ancient onychophores but antedating the appearance of chelicerates and mandibulates, the soft cuticle characteristic of the worm-like ancestor began to be replaced by a more rigid, unyielding, protective coat. Correlated with this development, several other changes must have occurred in the ancient groups. The problem of growth was eventually solved, in a manner of speaking, by perfection of the complex process of molting, with its implication of an endocrine system to integrate the activities of all parts of the body involved. The locomotion characteristic of the annelids, either by serpentine undulations or by reciprocal changes in the length and diameter of the body, could no longer be effected; the rigidly encased body could no longer bend or change its shape, except as flexible, intersegmental joints could be by chance developed and perpetuated through natural selection. Correlated with this event must have been changes in the musculature, the formerly extensive sheets of circular and longitudinal muscles being replaced by specifically acting groups of flexors and extensors, operating to bend one part of the body in relation to another. Also involved in this change in locomotion was the development of segmental appendages, with definite joints and muscle groups for their manipulation. With the development of the undifferentiated, generalized series of jointed appendages, capable of specific actions, it became possible for regional specialization to begin. Certain of the anterior segments, we may imagine, became incorporated into the primitive head, and their appendages were modified until they formed sense organs and mouth parts. Other segmental appendages in the long series must have become variously specialized as swimming paddles, chelipeds, and walking legs. Along with regional specialization, and the consequent partition of functions, must have occurred reduction in the number of somites; this would have been of survival value in that it led to the formation of a more compact and efficient body. It apparently involved coalescence of segments and their ganglia, as well as eventual elimination of anamorphic growth with its constant addition of posterior segments.

Similarly widespread changes occurred internally. Coelomic cavities suffered reduction and were replaced by the large blood spaces of the hemocoel. Segmental excretory organs associated with coelomic pouches became more and more restricted. In the crustacean stem these are now represented by a short and variable series of glandular structures, such as the green glands of the Malacostraca and the maxillary glands of more primitive forms. In chelicerates the coxal glands form a similar series of excretory organs, believed to represent modified nephridia.

All the foregoing changes were characteristic of aquatic arthropods and set the stage for the rise of the first terrestrial arthropods. In this important epoch, possession of an exoskeleton generally impervious to the passage of water, and of walking legs capable of supporting the weight of the body, took on a new significance. Through many thousands of years, random mutations and the selective action of the terrestrial environment brought about extensive internal modifications, notably in the systems concerned with excretion and respiration. Excretion in fresh-water arthropods involves a considerable expenditure of water, easily replaced from the surrounding medium. In terrestrial arthropods the necessity of water conservation made advantageous the suppression of the nephridial type of excretory organ and the perfection of Malpighian tubules. These organs eliminate excreta in a relatively dry state, and in the hind-gut the wastes are subjected to still further dehydration, the extracted water being returned to the blood. Onychophores, like earthworms, have retained nephridia and are restricted to moist terrestrial environments. Blood gills, the characteristic organs of gas exchange in aquatic forms, are too wasteful of water to be serviceable on land. Except in some terrestrial crustaceans, such as sow bugs, which cannot survive in really dry conditions, terrestrial arthropods have developed tracheal respiratory systems or book lungs. Both of these systems could develop through natural selection, having as their chief selective advantage the fact that they operate with very little loss of water by evaporation. The spiders and insects that have returned to life in fresh water, either as adults or as immature forms, have not regained the blood gills of their remote ancestors. They either carry with them films or bubbles of atmospheric air, as do many beetles and spiders; breathe at the surface, like mosquito larvae and pupae; or, like the naiads of the Odonata and other orders, develop tracheal gills.

To all of the adaptively advantageous modifications inherited from earlier terrestrial arthropods, insects have added yet another—the power of flight. Together with their complex, innate behavior patterns, this may be regarded as a major factor in the success of this group, as judged from their vast numbers and infinite diversity.

CHAPTER **16**

SPINY-SKINNED

The Phylum Echinodermata

The Echinodermata are non-segmented, triploblastic forms showing a five-part radial symmetry masking a fundamental bilaterality. Coelomic cavities are extensive, forming in the embryo as outpocketings of the primitive digestive tract. There is an endoskeleton composed of calcareous plates or spicules. A unique characteristic of echinoderms is the presence of a system of fluid-filled internal ducts, the so-called water-vascular system. In most echinoderms the blood-vascular system is so reduced as to be non-functional and very inconspicuous, and there are no traces of nephridial excretory organs.

The phylum may be divided into the subphylum **Pelmatozoa,** containing primitively stalked or attached forms, and the subphylum **Eleutherozoa,** including free-moving, unattached echinoderms. The Pelmatozoa, once very numerous, are now represented by only one modern class, the class **Crinoidea,** sea lilies and feather stars. Several other pelmatozoan classes, among them the **Cystoidea** and **Blastoidea,** contain extinct stalked forms known only as fossils (Fig. 16.1). The Eleutherozoa contain the remaining four classes of echinoderms: the class **Asteroidea,** sea stars or starfishes; the class **Ophiuroidea,** brittle stars, serpent stars, and basket stars; the class **Echinoidea,** sea urchins and sand dollars; and the class **Holothuroidea,** sea cucumbers.

Echinoderms are typically slow-moving, bottom-dwelling animals. They are exclusively marine, and there is no evidence from the fossil record that members of the phylum have ever become established in fresh water. Because of their radial symmetry, the echinoderms were at one time classed with the coelenterates as "zoophytes." Further study, however, showed that echinoderms are animals with an extensive coelom, which coelenterates lack, and that even their radial symmetry differs markedly from the coelenterate type. A significant feature of the life cycle of echinoderms is the occurrence of a segmented, bilaterally symmetrical larva, which develops by a complicated metamorphosis into the non-metameric, radially symmetrical adult. The structure of the adult presents many puzzling characteristics when compared with such familar types as mollusks, annelids, or chordates. If we interpret the evolution of echinoderms from the events in the life cycle of a

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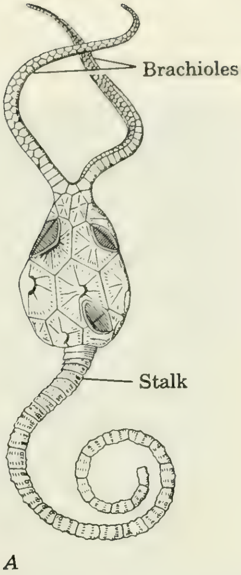


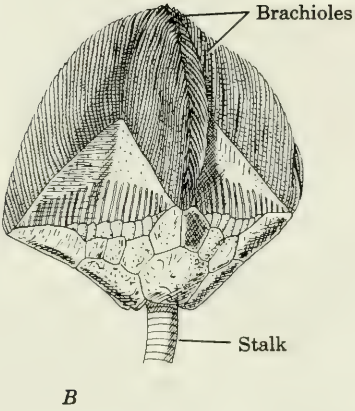
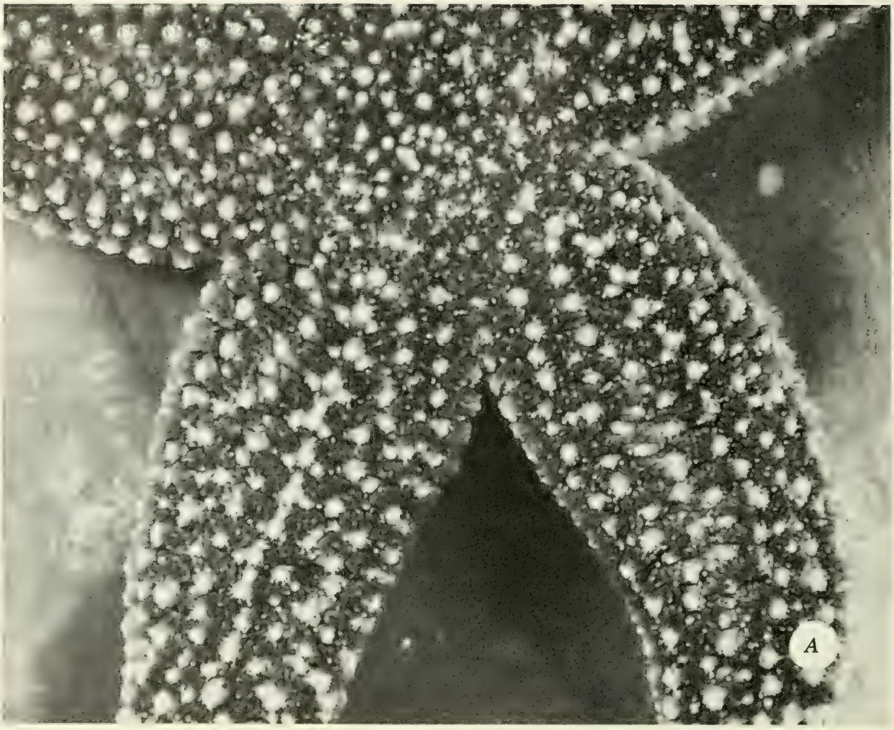


Fig. 16.1. Extinct stalked echinoderms. *A*, reconstruction of a cystoid, *Pleurocystites*, of Ordovician age. *B*, *Blastoidocrinus*, an Ordovician blastoid, reconstructed from fossil remains. *C*, fossil crinoids in a slab of Devonian limestone. For orientation in geological periods, see Figure 20.1. (*A*, redrawn after F. A. Bather, 1900, in Lankester's Treatise; *B*, redrawn from R. C. Moore, C. G. Lalicker, and A. G. Fischer, *Invertebrate Fossils*; copyright 1952 by McGraw-Hill Book Co., Inc., printed by permission; *C*, photograph courtesy Ward's Natural Science Establishment, Inc.)



typical representative such as the starfish, however, their morphological peculiarities become intelligible. The indications are that the remote ancestors of echinoderms were free-swimming, bilaterally symmetrical forms with segmentally arranged coelomic pouches. At some time long antedating the beginning of our fossil record, the ancestral forms apparently took up an attached way of life, and the secondary radial symmetry developed through some millions of years in connection with this fixed existence. The anatomical peculiarities of modern echinoderms, even of those that are no longer attached forms, are evidently related to these ancient adaptive changes. Embryological and serological evidence indicates that echinoderms are more closely related to the chordate evolutionary stem than to any other large group of animals (see Fig. 7.3, p. 219).

From an economic standpoint, echinoderms are unimportant, except for starfishes, which sometimes destroy whole beds of shellfish. One of the few echinoderms used as food by man is a sea cucumber, gathered, dried, and sold as *bêche-de-mer*, or **trepang.** Neither do echinoderms serve as food for many other animals; codfishes and related forms feed on starfishes, and the dugong, an aquatic mammal, eats sea cucumbers. On the whole, however, the spiny surfaces and the preponderance of skeletal material in the bodies of echinoderms have helped them avoid destruction by predatory enemies.

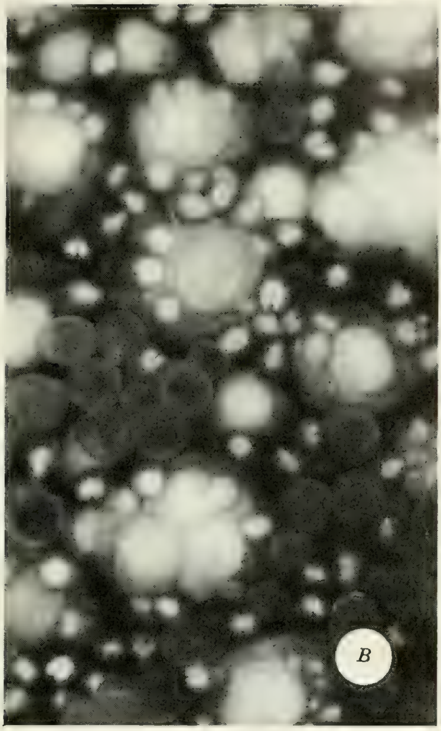


Fig. 16.2. External features of a starfish, *Asterias forbesi*. *A*, general view of the surface of the body, showing the prominent spines, the finger-like papulae or dermal branchiae, and the rosettes of small white pedicellariae surrounding the spines. *B*, small region of the body, highly magnified, showing these features in greater detail. Note the jaws of the pedicellariae and the distension of the papulae with circulating coelomic fluid. (Photographs by Bassett Maguire, Jr.)

In this chapter we shall review the structure and activities of various echinoderms from general and comparative points of view.

The Class Asteroidea

The Starfish: ***Structure and Activities.*** The commonest starfishes of the Atlantic coast of North America are species of the genus *Asterias; A. forbesi* occurs in shallow waters south of Cape Cod and is replaced in deeper waters and north of the Cape by *A. vulgaris*. In general, these animals are very similar. *Asterias forbesi* is found upon rocky and shelly bottoms, from high-tide mark to a depth of about 125 feet; in these zones the bivalve mollusks constituting the greater part of its food are most abundant. These starfishes sometimes occur on sandy or muddy bottoms and may crawl up wharf piles in search of food; on rocky shores they are often found in pools left by the receding tide.

The body consists of a central **disk** and five radiating **arms** or **rays** (Fig. 16.2). The upper or **aboral surface** is covered with short **spines**, which are skeletal structures; the surface between the spines bears thin-walled, finger-like projections called **papulae** or **dermal branchiae**, functioning in respiratory exchange and in excretion. Clustered at the bases of the spines and among the papulae are minute, pincer-like structures, the **pedicellariae,** which function in keeping the surface free of foreign matter. In such a sluggish, slow-moving animal as the starfish, this is a very important function indeed. In addition to finely divided particles of silt and detritus, the ocean is full of minute larvae of such forms as sponges, coelenterates, encrusting ectoprocts, and barnacles, seeking surfaces on which to settle and produce their characteristic growths. Starfishes are never encumbered by such growths, probably because of the activities of pedicellariae in removing them and keeping the papulae free of obstructions.

At one side of the disk, between the bases of two of the arms, lies a porous plate, the **madreporite** or **sieve plate;** through its minute openings the internal water-vascular system communicates with the exterior. For convenience in reference, the two arms between which the madreporite lies are termed the **bivium;** the other three are the **trivium.** On the **oral surface** the **mouth** occupies the center of the disk, surrounded by an oral membrane or **peristome.** Radiating from the mouth along the arms are five **ambulacral grooves,** from which project numerous locomotor organs called **tube feet.** At the outer end of each ambulacral groove lies a small, reddish **eye spot** below a short **sensory tentacle.**

The starfish creeps slowly along the bottom by coordinated stepping movements of its tube feet. Although it seems inflexible, and its arms may be broken off by rough handling, the animal can bend and twist in a great variety of ways. For example, when a starfish is turned upside-down, it rights itself by twisting the arms until some of the tube feet become attached to the bottom. Using these attached points for traction and for reference, the animal slowly turns itself back to the normal position. Changes in shape and attitude are brought about by the action of muscles which interconnect the calcareous plates of the body wall. Normal locomotion, however, is effected primarily by the tube feet, which in *Asterias* terminate in suckers and can be firmly attached to a hard substrate. Under certain conditions these suckers seem to be necessary, as when the animal clings to a wharf pile or stone or walks up the glass wall of an aquarium. But the animal can walk perfectly well without attaching its suckers, over a loose, sandy bottom or upon a greased surface, and the tube feet of many species of starfishes lack suckers altogether. The mechanism by which the tube feet operate will be explained in connection with the ambulacral system of which they are a part.

There is nothing like a head or an anterior end in the starfish; the animal can travel in any direction, and no part appears to assume the lead more frequently than others. Once the animal has started in a particular direction, however, the tube feet of all the arms step in the direction taken by those of the leading arm. The starfish thus progresses steadily until it encounters something to change the course of locomotion. A comparable coordination is shown in the righting reaction, when all the arms and their tube feet move in an integrated fashion as soon as a firm hold has been secured by some of the tube feet of one of the arms.

Structures and Functions Related to Metabolism and Responsiveness. The food of the starfish consists principally of mollusks, such as clams, oysters, scallops, and snails. In feeding, the animal assumes a characteristic "humped" position over the prey; the more proximal tube feet are attached by their suckers to the outer surface of the shell, and the more distal ones commonly appear to secure a hold upon the substrate. In some manner still imperfectly understood, the starfish soon causes the valves of the mollusk to gape open. An older theory, without any demonstrable basis, held that the starfish secretes some noxious substance which finds its way between the valves, paralyzing the adductor muscles of the bivalve. Experimental work has shown that by powerful, sustained contraction of its muscles (probably those connecting the ambulacral ossicles), the starfish can exert enough force through its firmly attached tube feet to pull the valves apart, at least a few millimeters. It is clear that such a small gape can be produced, without damaging the adductor muscles of the clam, by the application of a degree of force which the starfish is capable of bringing to bear on the valves. When even a small opening has been produced, the stomach of the starfish is everted through the mouth and inserted into the mantle cavity of the bivalve. It has been established by experiment that the folds of the everted stomach can pass through a surprisingly small orifice. Having penetrated the outer defenses of the clam, the starfish releases into the mantle cavity digestive enzymes so powerful that they gradually bring about the complete disintegration of the soft parts of the mollusk. The products of this extracellular digestion are conducted by powerful flagellary currents into the digestive cavity of the starfish. After completing its meal of the body of the mollusk, the starfish withdraws its stomach, closes its mouth, and crawls away, leaving behind only the empty shell of its prey. By this peculiar method of feeding, *Asterias forbesi* and *A. vulgaris* destroy large numbers of shellfish. One investigator reported that during a 6-day period, a single starfish devoured 56 clams, some as long as an arm of the starfish itself. Starfishes also feed on dead or injured animals other than shellfish and even attack other starfishes and sea urchins. In the absence of food, a starfish can survive starvation for several months.

The central portion of the **digestive system** occupies the short oral-aboral axis of the starfish (Fig. 16.3). The **mouth** opens into the **cardiac stomach**, the folded walls of which take up much of the cavity of the disk. Above the cardiac stomach, and communicating broadly with it, lies the small, flattened **pyloric stomach**, which leads upward into the short **intestine**. The intestine opens to the exterior at the **anus**, which is somewhat eccentrically placed on the aboral surface of the disk. The intestine bears a pair of branched, tubular organs, the **rectal caeca**, which lie between the roof of the pyloric stomach and the aboral body wall. These may be considered as homologous with the "water lungs" of holothurians (pp. 504–505), but their functions are unknown.

In addition to these central parts, the digestive tract also includes branched diverticula which extend into the cavities of the arms. These are the five

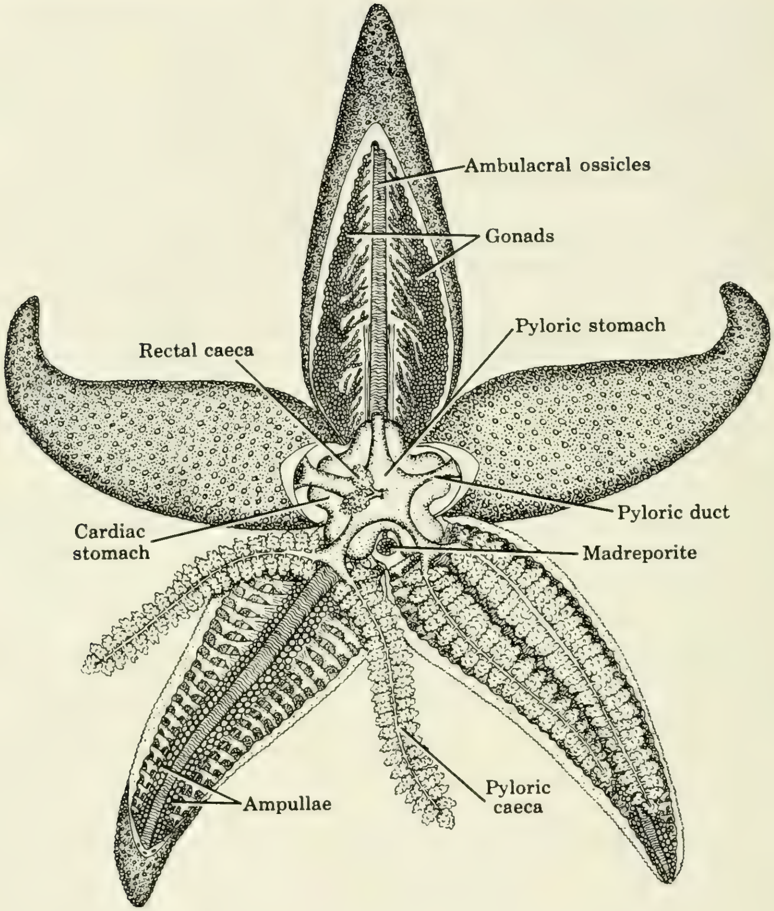

Ambulacral ossicles
Gonads
Pyloric stomach
Rectal caeca
Pyloric duct
Cardiac stomach
Madreporite
Ampullae
Pyloric caeca

Fig. 16.3. A starfish, *Asterias*, partially dissected from the aboral surface, to show relationships of various internal structures. (Redrawn from W. R. Coe, 1912, Geological and Natural History Survey, State of Connecticut, Bulletin 19.)

pairs of **pyloric caeca;** one pair lies in each arm, and a single duct leads from each pair into the pyloric stomach. The pyloric caeca consist of series of sac-like evaginations, extending along a central, tube-like canal. The walls of the sacs contain numerous glandular cells which are the apparent source of powerful digestive enzymes. Interspersed among the glandular elements are other cells, which function in the absorption of products of digestion and in the storage of reserves. All these cells together constitute a single-layered epithelium, like the lining of the intestine in a vertebrate. In the pyloric caeca, however, the cells bear long flagella which maintain a steady circulation of fluids within the cavities of the organs. Specifically directed currents sweep digestive juices toward the cardiac stomach, where the enzymes are principally active, and carry the products of digestion into the caeca for absorption.

The **coelomic fluid** contained in the extensive coelomic body cavities (Fig. 16.4) performs the functions of a circulatory system in the starfish. This colorless fluid contains many phagocytic, amoeboid cells and, very much like the hemocoelic blood of an arthropod, bathes the tissues of the body. In the starfish, however, there are no functional blood vessels, and there is no pulsatile heart. Circulation of the coelomic fluid is brought about by the action of flagella borne on the cells of the peritoneal lining. This single-layered epithelium covers both the inner surface of the body wall and the outer surfaces of all the organs. It is composed of cuboidal or flattened cells, each of which bears a single long flagellum. These flagella together maintain specific currents which prevent stagnation of the fluid and facilitate exchange of materials between the fluid and the tissues. Nutrients are passed into the coelomic fluid by the cells of the pyloric caeca, for transport to all other parts of the body; oxygen diffuses into the fluid through the thin-walled, finger-like papulae of the body wall and is carried in simple physical solution. Carbon dioxide and soluble nitrogenous excreta are transferred to the

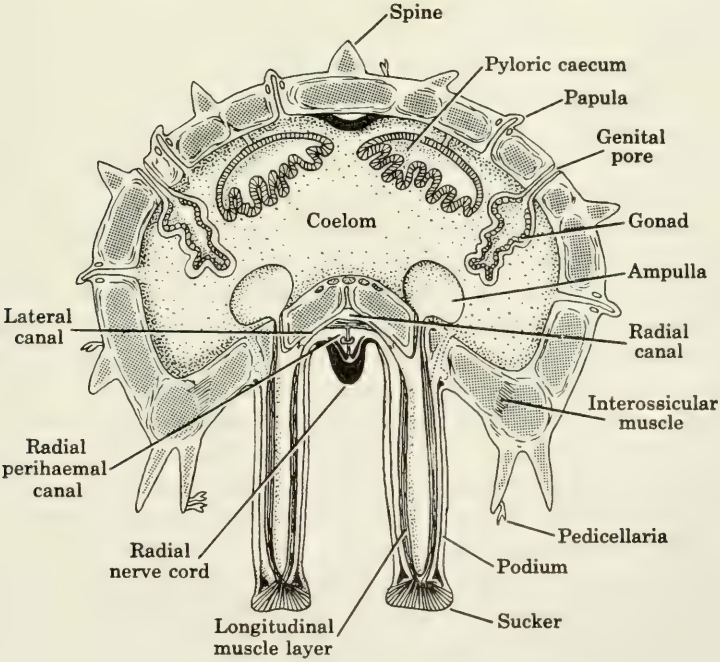

Spine
Pyloric caecum
Papula
Genital pore
Coelom
Gonad
Ampulla
Lateral canal
Radial canal
Interossicular muscle
Radial perihaemal canal
Pedicellaria
Radial nerve cord
Podium
Sucker
Longitudinal muscle layer

Fig. 16.4. Diagrammatic cross section of an arm of *Asterias*. Note that the genital pores, included in this drawing to show general relationships, actually lie very near the proximal end of the arm, in the angle between adjacent arms. (Redrawn, after H. C. Chadwick, from W. M. Reid in F. A. Brown, Jr., *et al.*, *Selected Invertebrate Types*, copyright 1950 by John Wiley and Sons, Inc., printed by permission.)

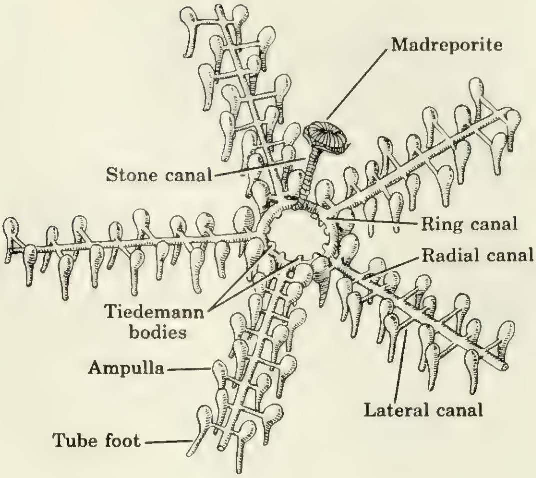
external sea water through the papulae, which thus function also as excretory organs. In general, it is clear that the circulating coelomic fluid performs the major functions which in most other animals are subserved by the circulating blood. This is particularly interesting, in view of the fact that, aside from small amounts of proteins and nutrients dissolved in it, the coelomic fluid is almost identical with sea water in its composition. In fact, certain organs of the starfish, notably isolated pyloric caeca, will survive for several days in cool, aerated sea water.

The **nervous system** of the starfish is basically organized on the radial plan typical of other parts of the body. Its chief components are a **circumoral nerve ring,** surrounding the peristomial membrane; a series of five **radial nerve cords,** one in each arm, extending from the nerve ring; and a generally distributed **subepidermal nerve plexus** with connections into the radial cords. In addition to the conspicuous eye spots and sensory tentacles at the tip of each arm, **receptors** are scattered throughout the epidermal layer. The nerve ring and radial cords, superficially located, consist of thickened and specialized areas of the epidermal layer (Fig. 16.4). They contain many neurons, arranged in sensory, association, and motor tracts. Aside from the circular and radial nerve cords, there are no true **nerves** in the starfish; nerve cell bodies are not restricted to the cords, and nerve fibers pass out from the cords more or less individually. The receptors that occur in the epidermis send afferent branches into the plexus layer, from which motor fibers run directly to muscles of the papulae, pedicellariae, and spines. Localized reflex activities of these structures are thus possible without the intervention of the "central" nervous system. More generalized responses involve afferent fiber tracts from the plexus into the radial cords, and complex efferent or motor pathways involving series of neurons that course from the cords to specific muscles of the body wall and tube feet. At the central end of each radial cord, the nerve ring contains a "motor center," a large group of nerve cell bodies which appear to be responsible for coordinating the activities of the tube feet in all the arms. In locomotion, the assumption by one arm of the "lead" position seems to involve a temporary dominance by the motor center of the leading arm over all the other motor centers. This condition is transitory, however, and the "lead" passes to other arms and their centers in turn.

The wall of the digestive tract contains a conspicuous nerve plexus layer, which undoubtedly has connections with visceral receptors and also with the muscle layers of the gut wall. The functions of this part of the nervous system have never been analyzed. Although the nervous system of the starfish presents many peculiarities, both structural and functional, the operation of this sytem is apparently fundamentally comparable with that of the nervous systems of other metazoans.

A unique feature of the anatomy of all echinoderms is the **water-vascular system,** or **ambulacral system** (Fig. 16.5). Through the projecting tube feet, the ambulacral system of the starfish functions chiefly in locomotion and in adherence to the substrate, although it may contribute significantly to the

Fig. 16.5. Diagram of the ambulacral system of *Asterias.* (Redrawn from W. R. Coe, 1912, Geological and Natural History Survey, State of Connecticut, Bulletin 19.)



process of respiratory exchange also. The **madreporite,** lying on the aboral surface of the disk, contains many small openings into a tube, the **stone canal,** which passes orally and joins a circular **ring canal** around the mouth. From the ring canal a **radial canal** extends to the tip of each arm, passing just above the radial nerve cord. At frequent intervals the radial canal gives rise to short **lateral canals,** each of which terminates in a tube foot. At its inner end each tube foot bears a muscular bulb, the **ampulla;** the stalk of the tube foot projects through the body wall, passing between the closely set skeletal plates. The system as a whole contains a fluid which, like the coelomic fluid, is practically identical with sea water. Circulation through the system is maintained by the action of flagella on the lining epithelium. The arrangement is such that the fluid contents of the system may pass freely into each tube foot through the lateral canal, and within the tube foot may flow back and forth between the stalk and the ampulla. Backflow from the tube foot into the lateral canal is prevented by a valve-like structure. The wall of the stalk contains longitudinal muscle fibers, and the terminal disk or sucker is provided with muscle fibers whose contraction raises the central portion of the disk to provide a vacuum for attachment to the substrate. The longitudinal muscles are basally attached in a radial fashion to the adjacent skeletal plates of the body wall. These so-called "postural muscles" provide for the pointing of the tube foot in any direction and thus allow directed locomotion. The complex interactions of the musculature are reflexly coordinated: contraction of the muscles of the ampulla forces fluid into the stalk, causing it to extend in a direction determined by the state of the postural muscles; the sucker is then placed on the substrate and attached by contraction of its special muscles. As the body moves forward, the sucker is released, and contraction of the longitudinal muscles of the stalk forces fluid back into the ampulla and brings about retraction of the stalk. The cycle

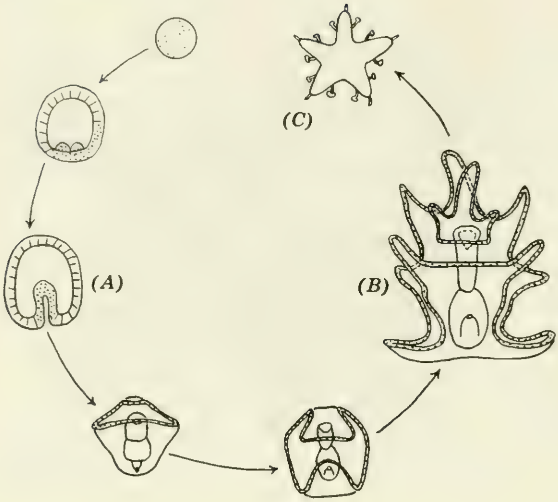


Fig. 16.6. Generalized, schematic life cycle of an asteroid echinoderm. The gastrula (*A*) transforms through intermediate stages into a bipinnaria larva (*B*), which metamorphoses into a young starfish (*C*). (Adapted from H. Barraclough Fell, 1948, *Biological Reviews*, vol. 23, printed by permission of the Cambridge University Press.)

is then repeated through a new stepping sequence. The integration of all these activities involves the coordinating functions of the central nervous system.

The **skeletal system** is of mesodermal origin and lies beneath the epidermis of the body wall. It is thus an **endoskeleton**, showing similarities to the skeleton of a vertebrate, rather than a cuticular exoskeleton of the type more common among invertebrate animals. The plasticity of the body, as shown in righting and other activities, is accounted for by the fact that the skeleton of the starfish is composed of many small plates, bound together by connective tissue and muscle fibers.

The Reproductive System, Reproduction, and Development. Starfishes are dioecious. The **reproductive system** consists of five pairs of **gonads**, either ovaries or testes, one pair lying in the coelomic cavity of each arm, lateral to the pyloric caeca. Each gonad is continuous with a short stalk which forms its duct and attaches it to the body wall. The ducts open to the outside at **genital pores** located deep in the angles between the bases of adjacent arms. Gametes are discharged into the sea, where fertilization occurs. The eggs, and thus the zygotes, contain very little yolk, and cleavage is total and equal. Development proceeds rapidly through blastula and gastrula stages, the gastrula soon transforming into a bilateral, ciliated larva, the **bipinnaria** (Fig. 16.6). This larva has a complete digestive tract and feeds on unicellular algae as it swims about near the surface. Its free life may last for several weeks. Finally, the larva sinks to the bottom, becomes temporarily attached, and undergoes a radical metamorphosis into a tiny starfish. In the course of this metamorphosis, the organization of the larva changes completely. The left side of the larva becomes the oral surface of the adult; the old openings of the digestive tract disappear, to be replaced by a new mouth and anus in shifted locations. The paired coelomic sacs of the larva are transformed into specific adult structures: one of the pouches establishes an external connection, the future madreporite, and develops into the water-vascular system; other pouches give rise to various parts of the spacious perivisceral coelom of the adult. It is perhaps significant, in interpreting the evolution of echinoderms, that the change from bilaterality to radial symmetry in the starfish occurs during a temporarily attached phase of the life cycle.

Regeneration. Starfishes are often found in nature with one or more arms smaller than the rest. The small arms are in the process of regeneration. Under experimental conditions as many as four arms may be removed without causing the death of the animal, and all four can eventually be replaced by regeneration. When all five arms are removed, regeneration can still occur if the individual is fed after the formation of the new arms has begun. Although an isolated arm of *Asterias* can survive for several weeks, it will eventually die, since it cannot restore the disk and other arms. In some other starfishes, however, even a single isolated arm has the capacity to regenerate into a complete individual. Under rough or damaging treatment a starfish may shed an injured or restrained arm by a process termed **autotomy.** A break of this kind always occurs at the base of the arm, where the body cavity is restricted as it passes from disk to arm. The resultant opening in the side of the disk is immediately closed by the contraction of the adjacent body-wall musculature, and regenerative changes then begin.

Other Asteroidea. In all the members of the class Asteroidea, the body is stellate, whether the arms are long and slender, as in *Henricia*, or short and broad, as in *Oreaster*. In some species more than five arms are present, as in *Solaster*. In the leather stars, *Dermasterias*, spines are lacking, and the body is covered by a smooth skin concealing the underlying reduced skeleton. There are few members of the class so modified that they are not immediately recognizable as asteroids.

The Class Ophiuroidea

Members of this class, the so-called serpent stars, brittle stars, and basket stars, are recognizable by the relatively large and conspicuous disk and the slender, mobile arms (Fig. 16.7). In basket stars the arms branch repeatedly and terminate in many small, flexible tendrils. In ophiuroids the organs of the digestive tract do not extend into the arms; the volume of the skeleton is relatively much greater than in the asteroids, and the arms are largely occupied by jointed skeletal units sometimes called "vertebrae." Brittle stars are so named because of the fragility of their arms, which lash about actively and break off very easily. In spite of their peculiarities, the ophiuroids are clearly echinoderms. The life cycle (Fig. 16.8) includes a bilateral, ciliated

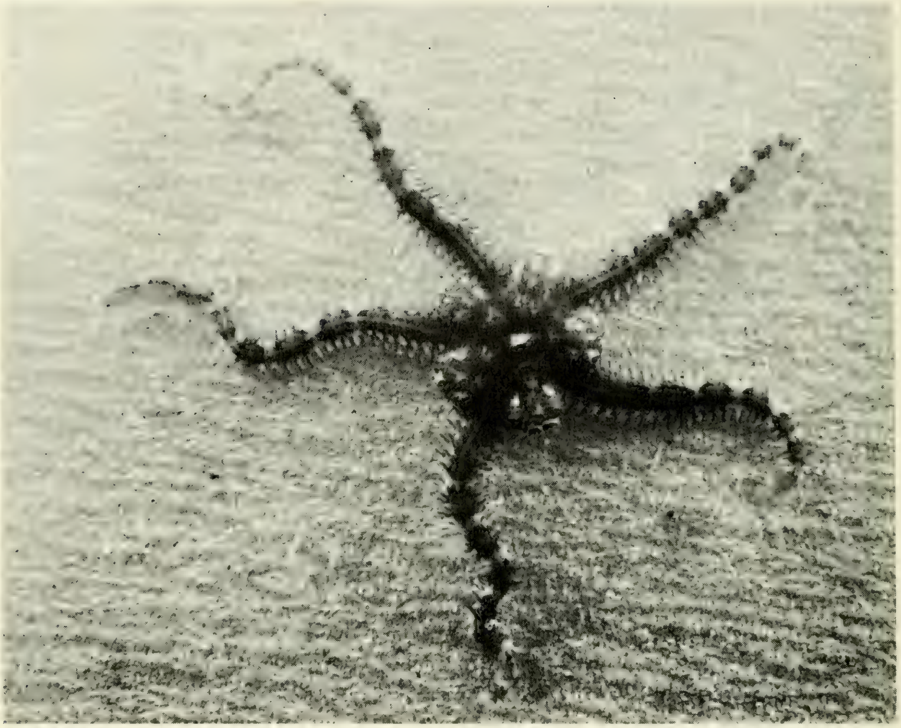


Fig. 16.7. Class Ophiuroidea. A brittle star, *Ophiopholis aculeata;* note the characteristic sharp distinction between the bulbous central disk and the slender, flexible arms. (Photograph by George Lower.)

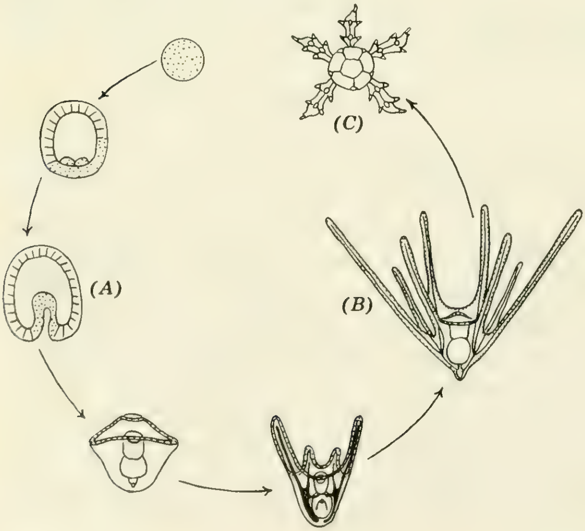


Fig. 16.8. Generalized, schematic life cycle of an ophiuroid echinoderm. The gastrula (*A*) transforms through an indifferent pluteus stage into a fully developed **ophiopluteus** larva (*B*), which undergoes metamorphosis into a young brittle star. (Adapted from H. B. Fell, 1948, *Biological Reviews*, vol. 23, printed by permission of the Cambridge University Press.)

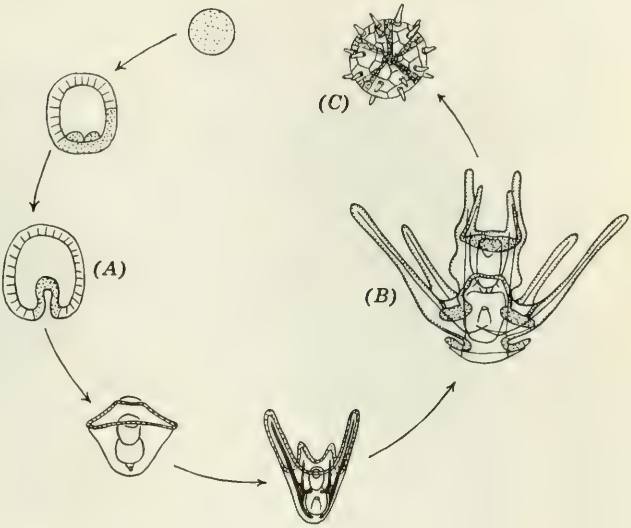


Fig. 16.10. Generalized, schematic life cycle of an echinoid echinoderm. Through an indifferent pluteus stage the gastrula (*A*) transforms into a fully developed **echinopluteus** (*B*); after a period of larval life this metamorphoses into a young sea urchin (*C*). (Adapted from H. B. Fell, 1948, *Biological Reviews*, vol. 23, printed by permission of the Cambridge University Press.)

radial appendages of the digestive system as in the starfish. Aside from these special features, however, the internal organization is similar to that of the asteroids: the ambulacral and reproductive systems, as well as the nervous system, are generally comparable in arrangement to those of the starfish, although the circulatory system is better developed.

In *Arbacia* the sexes are separate; the five gonads are radially arranged, and each sheds its sexual products into the sea water through one of the pores located on the genital plates. Fertilization is thus external, and development proceeds rapidly to a bilateral, ciliated larval stage, the **echinopluteus** (Fig. 16.10). This larva is comparable to the bipinnaria of the starfish, although in the presence of several pairs of long arms, each supported by an internal spine, it resembles even more closely the ophiopluteus of the ophiuroids. After several weeks of pelagic life, feeding on diatoms and microscopic algae, the pluteus sinks to the bottom and undergoes metamorphosis into a miniature sea urchin.

Other Echinoidea. In *Arbacia* the body is circular in its lateral outline, and the 20 rows of plates are arranged in a regular pattern. This regularity of skeletal arrangement has not always been characteristic of sea urchins, as shown by some fossil forms in which the plates are irregularly arranged. Among the modern echinoids the shape and symmetry of the body are highly variable (Fig. 16.11). In *Clypeaster* the mouth is in the center of the oral surface, but the anus lies in an interambulacral area on the lateral margin of the somewhat flattened body; thus the animal is actually bilaterally symmetrical. In the sand dollar, *Echinarachnius parma*, the organization is like that of the clypeasters, although the flattening of the body is more extreme. In the type represented by *Spatangus*, the mouth has shifted peripherally, or

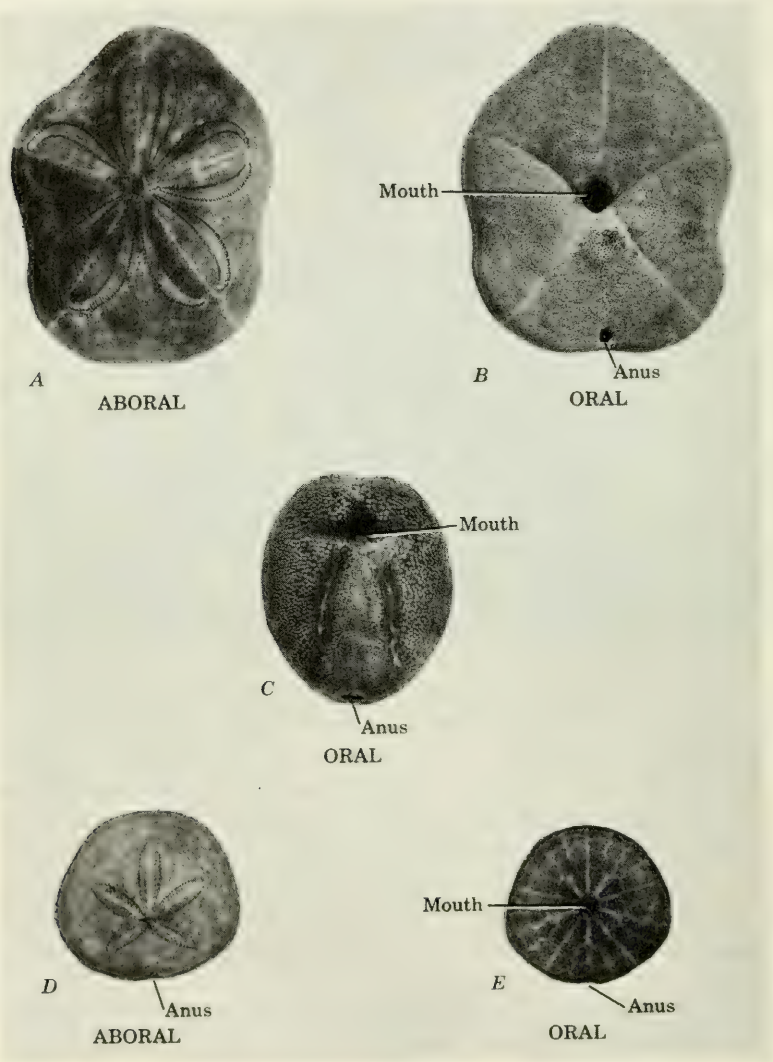

Mouth
Anus
A
ABORAL
B
ORAL
Mouth
C
Anus
ORAL
D
Anus
ABORAL
Mouth
E
Anus
ORAL

Fig. 16.11. Cleaned tests of some echinoids which approach bilateral symmetry in some external features. *A* and *B*, a sand dollar, *Clypeaster*, in which both mouth and anus lie on the "median plane" of the oral surface. *C*, a heart urchin, *Spatangus*, with the mouth displaced "anteriorly" and the anus at the opposite end of the body. *D* and *E*, a sand dollar, *Echinarachnius*, with the mouth centrally located and the anus at the "posterior" edge of the flattened body. These modifications may be interpreted in relation to the habits of the animals, which either inhabit burrows or live just under the surface of sandy bottoms.

in an "anterior" direction, along the ambulacral area opposite the anus. The fossil record and the life cycles of these bilateral urchins indicate that they have descended from ancestors which were circular and radial like *Arbacia*. The existence of fossil forms with irregularly arranged plates suggests, in turn, that the *Arbacia* type, with 20 rows regularly arranged, arose from ancestors without this skeletal regularity.

The Class Holothuroidea

The Sea Cucumber. *Thyone briareus*, a sea cucumber common along the Atlantic coast from Cape Cod southward, is an example of the holothurian type of echinoderm (Fig. 16.12). Fundamentally, it is radially symmetrical, but the characteristic elongation of the body between oral and aboral ends, and certain other specializations, give it a bilateral and often worm-like appearance. The texture of the body is very different from that found in the starfish and sea urchin: the expanded *Thyone* is soft, like a bladder partly distended with fluid, and there is no skeleton except minute calcareous spicules embedded in the body wall and a few larger plates in the oral region. At one end is the **mouth**, surrounded by ten branched **tentacles**, and at the other is the **anus**. The **tube feet** are not in distinct rows but lie scattered all over the body, although internally they are connected with five

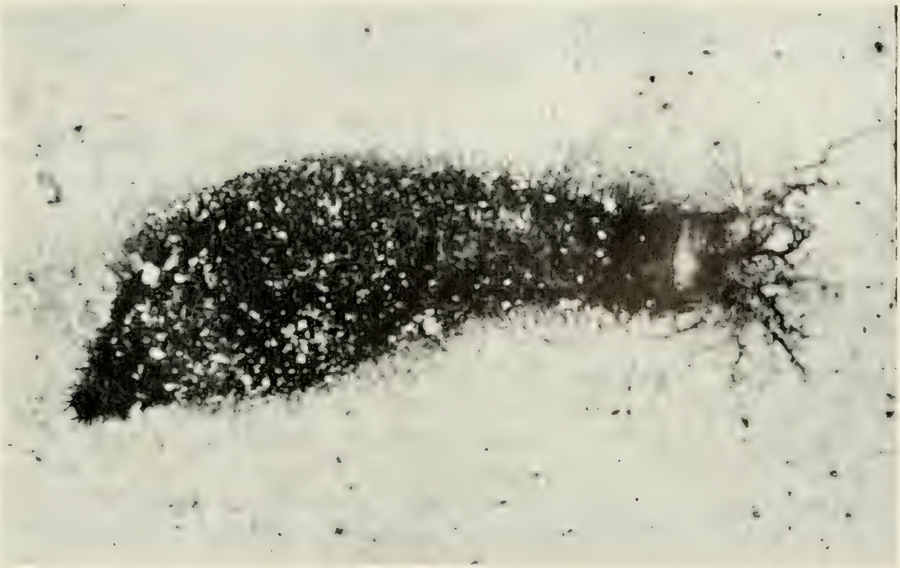


Fig. 16.12. A sea cucumber, *Thyone briareus*. In this individual the feeding tentacles are well extended; note also the sand grains adhering to the tube feet, scattered irregularly over the surface of the body. (Photograph by George Lower.)

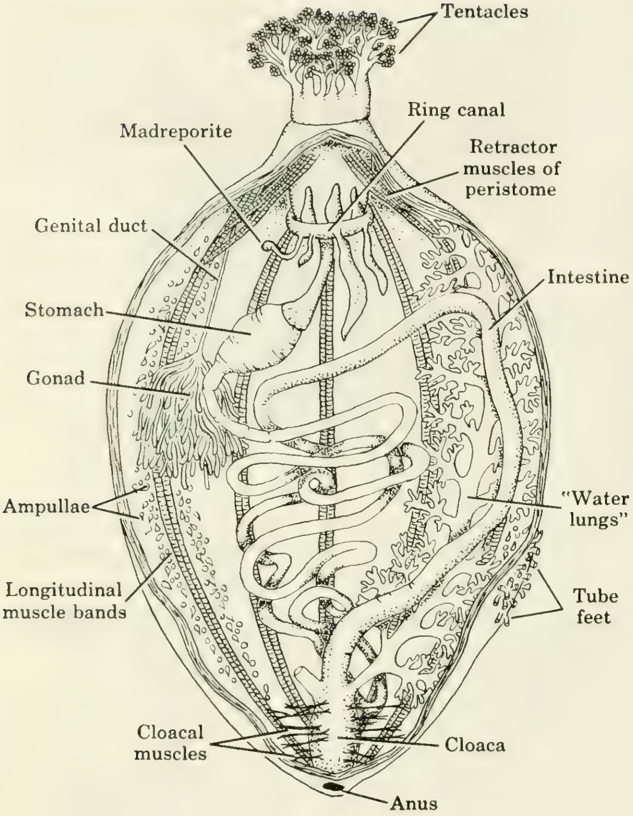

Tentacles
Ring canal
Madreporite
Retractor muscles of peristome
Genital duct
Intestine
Stomach
Gonad
Ampullae
"Water lungs"
Longitudinal muscle bands
Tube feet
Cloacal muscles
Cloaca
Anus

Fig. 16.13. Internal anatomy of a sea cucumber, *Thyone briareus*. One of the "water lungs," or respiratory trees, has been removed, and the mesenteries supporting the digestive tract are not shown. Note that the madreporite opens into the perivisceral coelom, not externally. (Redrawn from W. M. Reid in F. A. Brown, Jr., *et al.*, *Selected Invertebrate Types*, copyright 1950 by John Wiley and Sons, Inc., printed by permission.)

radial ambulacral canals as in other echinoderms. The animal usually lies on one side, and this "ventral" surface has larger and more numerous tube feet than the "dorsal" or uppermost side. In addition, the distance from mouth to anus is greater along the ventral midline than along the dorsal; and to this extent *Thyone* presents a bilateral appearance, with dorsoventral as well as anteroposterior differentiation.

Thyone lives partly embedded in the ooze of muddy bottoms just below low-tide level, with its anterior and posterior ends exposed. The anterior end is directed diagonally upward, and the tentacles are free to move over the surface of the surrounding mud. If the animal is disturbed, the tentacles are withdrawn by inversion of the entire oral end of the body; excess water is discharged from the anus, and the body becomes tense and turgid. In feeding, the tentacles are moved about until well covered with silt from the bottom and are then thrust, one at a time, deep within the mouth and relieved of their burden as they are again withdrawn. The animal "breathes" sea water, pumping it in and out through the anus. In locomotion, the organism moves by extending its tube feet, attaching their terminal suckers, and dragging itself along. By this means it can even walk up the glass side of an aquarium.

The **digestive system** begins as a small, muscular **pharynx,** surrounded by the tough, ring-like structure to which the tentacles are attached, and which can be retracted by the contraction of five stout muscles running to the body wall (Fig. 16.13). The pharynx is followed by a short **esophagus,** a small muscular **stomach,** and a long, looped **intestine.** The intestine traverses the length of the coelomic cavity three times, supported along part of its course by dorsal and ventral mesenteries containing blood vessels. At its posterior end, the intestine enlarges to form the **cloaca,** which opens to the exterior at the anus. The cloaca bears a pair of branching, tubular structures, the "water lungs," which are filled with water drawn through the anus and pumped into them by cloacal contractions. Through the walls of these tubules respiratory exchange occurs between the water and the coelomic fluid, and the water is periodically expelled by contraction of the body wall.

Thyone shows peculiarities in other organ systems. The **ambulacral system** consists of the same parts found in the starfish and the sea urchin, arranged somewhat differently. The ampullae of the tube feet are scattered over the internal surface of the body wall but connect with five radial ambulacral canals. The stone canal springs from the ring canal about the pharynx and ends in an internal madreporite, which hangs free in the coelomic cavity and has no external openings. A so-called **haemal system,** very rudimentary in other echinoderms, is well developed in holothurians. In *Thyone* it is particularly conspicuous in connection with the digestive tract, to which branches of the haemal system run in the mesenteries. Although there is no heart or other propulsive organ, the haemal system contains a fluid which probably

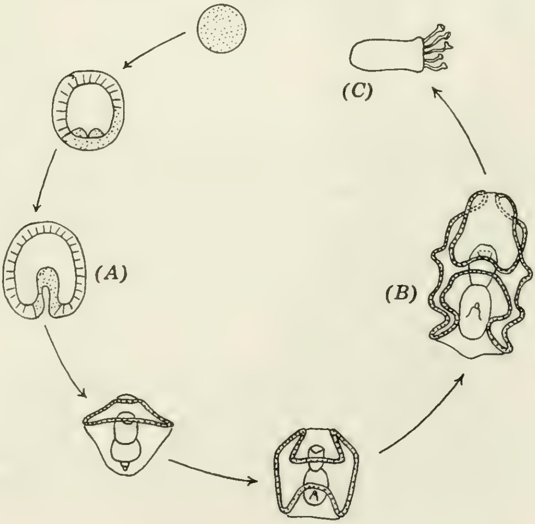


Fig. 16.14. Generalized, schematic life cycle of a holothuroid echinoderm. Through intermediate stages essentially similar to those of an asteroid, the gastrula (*A*) transforms into an auricularia larva (*B*); this later metamorphoses into a young sea cucumber (*C*). (Adapted from H. B. Fell, 1948, *Biological Reviews*, vol. 23, printed by permission of the Cambridge University Press.)

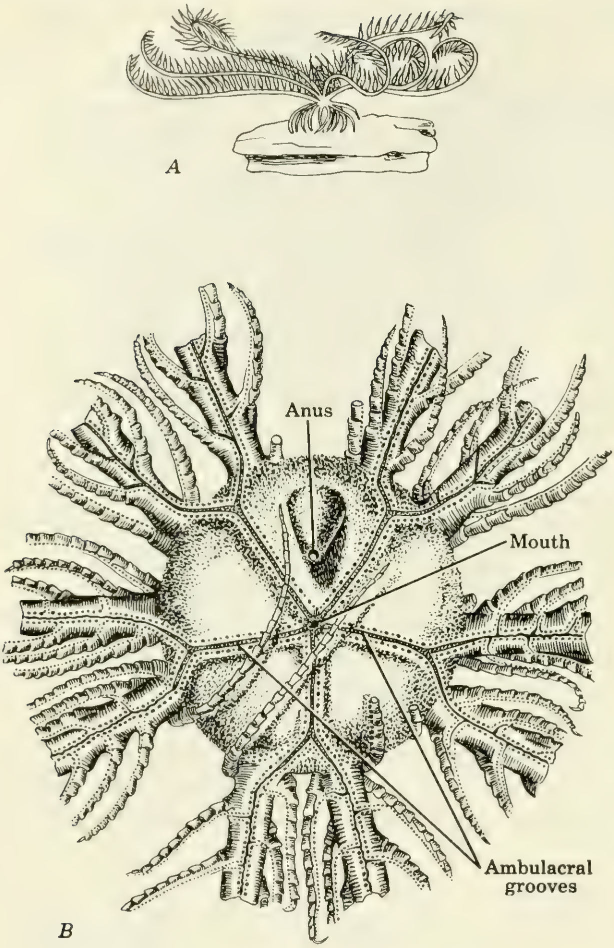


Fig. 16.15. Class Crinoidea. A feather star, *Antedon rosaceus*. *A*, general appearance of the animal. *B*, oral view of the central disk, showing the ambulacral grooves converging on the mouth. The anus is elevated on a conical structure. (Redrawn from H. C. Chadwick, 1907, *Liverpool Marine Biological Committee Memoirs*, no. 15.)

circulates and serves some of the functions of a blood-vascular system. As in other echinoderms, however, the coelomic fluid is most important in this respect. The **reproductive system** in holothurians is peculiar in that there is only one gonad, the duct of which opens externally in the dorsal interambulacral area between two of the tentacles. The animals are dioecious; gametes are shed into the sea, fertilization is external, and as in other echinoderms there is a bilateral, ciliated larval stage, called in this instance the **auricularia** (Fig. 16.14).

If its lack of a skeleton is disregarded, a sea cucumber is like a sea urchin with its body elongated in the axis of radial symmetry, which extends from mouth to anus. Correlated with this elongation are the anteroposterior and dorsoventral differentiations and the appearance of a superficial bilateral symmetry.

Other Holothuroidea. *Thyone* and *Cucumaria*, a species with five distinct rows of tube feet, represent a type of sea cucumber in which the body form is not highly specialized by extreme modifications and loss of parts. In contrast, *Leptosynapta*, a burrowing type, lacks tube feet altogether; its echinoderm characteristics are revealed, however, by the presence of minute skeletal plates and five radial muscle bands, visible through the translucent body wall. One of the more highly modified holothurian types is represented by *Psolus chitinoides*, a species common on the North Pacific coast. In this form the dorsal surface is protected by scale-like skeletal plates, and the ventral surface resembles the creeping foot of a mollusk, except for the presence of three rows of tube feet.

The Class Crinoidea

Members of the class Crinoidea have branched arms and are often attached to the bottom by a stalk, which joins the aboral surface of the disk. This gives the animal a flower-like appearance and is responsible for the common name, "sea lily." Even the type represented by *Antedon*, the so-called feather star, which has no stalk and is not permanently attached, bears a tuft of aboral filaments by which it commonly clings to the substrate (Fig. 16.15). In all crinoids, the oral surface is uppermost; the mouth occupies the center of the oral surface of the disk, surrounded by five highly branched arms. The anus also lies on the oral surface, near the mouth, at the tip of an anal papilla. Ciliated ambulacral grooves radiate from the mouth, traversing the

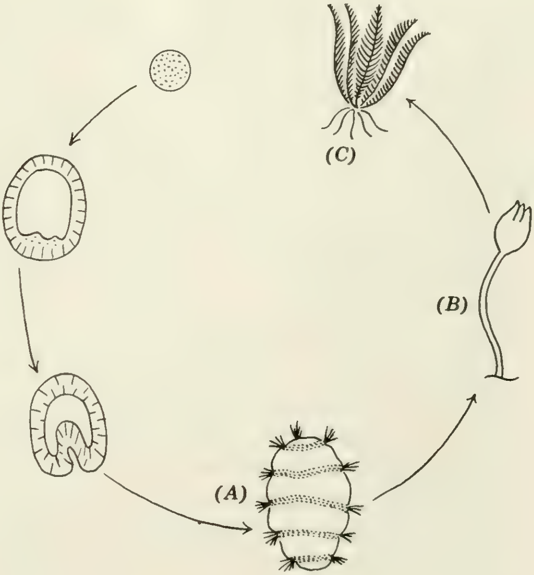


Fig. 16.16. Generalized, schematic life cycle of a crinoid, based on *Antedon*. The free-swimming larva (*A*) is relatively undifferentiated; it attaches and transforms into a **pentacrinoid** stage (*B*), which later metamorphoses into a free-swimming feather star (*C*). (Adapted from H. B. Fell, 1948, *Biological Reviews*, vol. 23, printed by permission of the Cambridge University Press.)

disk and continuing along the oral surfaces of the arms and their branches (Fig. 16.15). Currents maintained in these grooves converge upon the mouth and carry into it the microscopic particulate matter which constitutes the food of the crinoids. Tube feet are present, but they lack ampullae and terminal suckers; they have tactile functions and serve also in respiratory exchange. As in holothurians, the water-vascular system of the adult crinoid has no external madreporite; there are multiple "water tubes" or stone canals which furnish communications between the ambulacral ring canal and the coelomic cavity.

The life cycle of the crinoids is best known for the feather star (Fig. 16.16). It includes a barrel-shaped, ciliated larva which, though simplified, is comparable with the larvae of other echinoderms. After a free-swimming period, this larva becomes attached and undergoes metamorphosis into a juvenile form with a jointed stalk like that of the sea lilies. Eventually, the connection between the stalk and the disk is broken, and the animal becomes free-moving. This stalked phase in the life cycle of *Antedon* indicates that feather stars have evolved from ancestors attached throughout their adult life. The fossil record shows that stalked crinoids have had an extremely long evolutionary history, dating from the end of the Cambrian period. Different crinoid groups have flourished during successive geological eras; most of them were stalked forms, and by far the majority have become extinct. The modern crinoid fauna is dominated by the free-moving feather star type.

The Echinoderm Body Plan

When compared with the organization of other eucoelomate metazoans, the body plan of a typical echinoderm appears in some respects highly aberrant. Examination of details reveals, however, that there are more similarities than differences between echinoderms and other eucoelomate animals. As is typical of all, echinoderms are triploblastic and have a well-developed coelom. Moreover, the arrangement of tissues in the body wall and in the wall of the gut in an echinoderm is fundamentally like the arrangement in such other metazoans as annelids and vertebrates. In each of these forms the body wall is covered externally by an epidermis and internally by a peritoneum, and between these two layers are muscular and connective tissues. The wall of the digestive tract in each type consists of a covering peritoneum, a region of muscular and connective tissues, and a lining of columnar epithelium. Furthermore, these tissues arise from similar germ layers in the embryonic development of these different forms, in ways which differ only slightly among the three. Considering these and other general correspondences, it is clear that the major dissimilarities stem from the fact that, unlike all other eucoelomates, echinoderms are organized on a radially symmetrical plan.

If, in addition, the bilateral larva and its probable evolutionary significance are considered, the body of an adult echinoderm may be interpreted as an extreme modification of the bilateral-triploblastic-eucoelomate plan which appears in all the more highly developed phyla —a modification which involved the remodelling of typical bilateral organization along the lines of radial symmetry. The larvae (bipinnaria, pluteus, auricularia, etc.) characteristic of the various classes show many similarities, and it has been suggested that they may all have arisen from a hypothetical ancestral larval form called the **dipleurula.**

But how does it happen that an animal which is radially symmetrical as an adult has a bilateral larva? Two answers may be considered. Either this larval stage has developed secondarily and represents what happened to be produced in the adjustments of larval life during the long evolutionary history of the echinoderms; or, more probably, it occurs in the development of echinoderms because it represents a stage in their ancestry, like the fish-like stages in the ontogeny of a higher vertebrate. If we regard a dipleurula-like animal as representing a bilaterally symmetrical ancestor of echinoderms, we may suppose that this ancestor became attached and acquired a five-part radial symmetry in correlation with a sessile way of life. The oldest known echinoderm fossils represent attached forms, and the fixed habit has been retained by modern crinoid sea lilies. The ancestors of asteroids, ophiuroids, holothurians, and echinoids, on the other hand, no longer attached forms, have become variously modified for free life. But even the free-moving asteroids and feather stars show a temporary attached phase at the time in the life cycle when the bilaterality of the larva is replaced by the radial symmetry of the adult. Finally, it should be noted that in some holothurians and sea urchins, the secondary radial symmetry has begun to be replaced by a new bilaterality, which is unrelated to the bilateral symmetry of their larvae.

CHAPTER 17

THE VITAL FUNCTIONS AND ORGAN SYSTEMS OF INVERTEBRATES

The vital functions and organ systems of vertebrate animals have been discussed in the early chapters of this book, and in subsequent chapters comparisons have been drawn between the organ systems of vertebrates and the structures serving similar functions in invertebrates. Let us now consider the functional systems of invertebrates in more general terms; such a survey will illustrate the kind of diversity and unity that is everywhere apparent when the world of animal life is carefully studied. Often the plan of an organ system is remarkably similar throughout a considerable number of phyla. But in other phyla the varied structural relationships clearly indicate that the systems in these phyla are not homologous, although non-homologous parts may be functionally analogous. It should be recalled that the simpler and more primitive types of invertebrate animals do not possess organ systems, if we define these as **groups of organs** which, taken as a whole, perform some common function. Indeed, the simpler animals may even lack **organs**, and the simplest types of metazoans have not evolved **tissues**. Nevertheless, one important generalization emerges from comparative studies of invertebrates, and this will be the theme of the present chapter. All animals, of whatever grade of complexity, are (figuratively speaking) faced with certain basic problems of existence; and different groups of animals have solved these common problems in a variety of ways, utilizing the structural possibilities available to them within their particular levels of organization. For example, the metabolism of all animals imposes certain general requirements: all animals must have sources of energy to maintain their metabolic reactions. In simple, plant-like protozoans, energy-rich compounds are manufactured by a photosynthetic process; in more typical animals, metabolic requirements are met by the many activities involved in the capture, ingestion, digestion, absorption, circulation, and assimilation of energy-rich compounds which

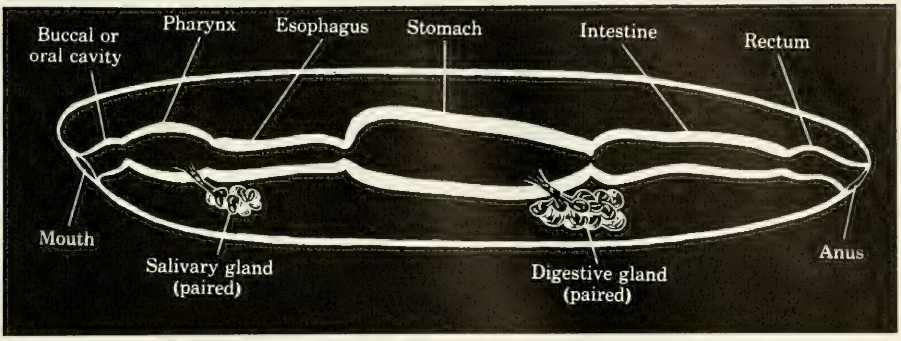


Fig. 17.1. Schematic diagram of the generalized digestive system in invertebrates.

serve as food. These reactions tend to become more elaborate, or to be served by more elaborate structural specializations, as the size and complexity of animals increase. Holozoic animals ingest many kinds of food, and their digestive mechanisms are correspondingly adapted, both structurally and functionally, to their individual necessities. And yet, in all animals that have digestive tracts, the digestive systems show obvious similarities; in fact, the digestive system has much the same fundamental structure in all animals that have both mouth and anus. In contrast, the reproductive systems of the different phyla show great diversity of structure, although there are remarkable functional parallels. Thus, to return to our figure of speech, the problem of developing an efficient reproductive system has been solved in a great variety of ways.

The comparative review to be undertaken in the present chapter furnishes data for consideration by the student of evolution, although little reference will be made to this aspect of the subject. It should become evident, however, that homologous structures may be modified for diverse functions, and that structures of varied embryonic origins may be adapted to common functional purposes.

Systems Related to Metabolism

Digestive Systems. Members of the phylum Protozoa perform all of their vital activities at the unicellular level, and their structural specializations for various functions are often referred to as organelles. In the more complex protozoans, such as the paramecium, there is a "system" of organelles specialized for various aspects of nutrition. The cytostome or cell mouth, the gullet, and the anal spot where egestion occurs are permanent features of the cell, along with certain modifications of the oral ciliation used in feeding. The food vacuoles, on the other hand, are not permanent but transitory. The amoeba possesses only temporary structures, the food vacuoles and the pseudopodia. The available evidence indicates that the particles of food contained in food vacuoles are subjected to enzymatic hydrolysis, or digestion, and that the functions of the food vacuoles are thus those of "temporary stomachs."

In the Mesozoa and Porifera there is no enteron, or digestive cavity; mesozoans absorb food in solution through the cells of the outer layer, and sponges ingest particulate matter through the activities of individual collar cells lining the water channels. In the Coelenterata, Ctenophora, and Platyhelminthes, the enteron is a cavity, usually with only one external opening. If we define a digestive tract as a continuous tube through which food moves from mouth to anus, these groups have not evolved true digestive tracts. In the other phyla of invertebrates there is, typically, a complete enteron with both mouth and anus, and the term digestive tract is applicable. It is interesting to note that in some protozoans a tract-like course is followed by the food vacuoles as they traverse the cytoplasm of the single-celled body. The intracellular digestion which occurs in protozoans and in the digestive cells of many metazoans presents another parallel between unicellular and multicellular animals.

As we pass on to the invertebrates with complete digestive tracts, with both mouth and anus, it is clear that a fundamental plan is characteristic of all. Once the tubular digestive tract had been evolved in its basic aspects, it was apparently preserved in all subsequent groups through the selective advantages it presents. Comparisons may be made by means of a generalized diagram such as Figure 17.1. This is a schematic representation of an invertebrate digestive system with all the important parts that might be found in a single species. Certain invertebrates have all these parts, but in most species some are missing whereas others are highly developed. There is probably no organ system of animals which demonstrates more clearly than the digestive system the relation between structure and function. Digestive systems are adapted to many different kinds of food, therefore to many ways of feeding and the related requirements of digestion. Parts that are necessary for ingestion and digestion in some species may be unnecessary in others, and so may be absent or reduced, even in species within the same phylum. For example, compare the digestive system of the clamworm, a predaceous, free-swimming annelid (pp. 398–399), with that of the earthworm, a comparatively sedentary, herbivorous annelid (pp. 405 406). The digestive systems of forms described in preceding chapters may be effectively reviewed by comparisons with the schematic figure.

With respect to functions, the tubular digestive tract shows regional specializations related to various aspects of the digestive process. The mouth parts, oral cavity, and pharynx are concerned chiefly with **ingestion**;

the esophagus is a passageway; the stomach is the place where **digestion** and **absorption** begin; the intestine is the region where these processes are completed; and the terminal region called the rectum forms feces for **egestion** and may have special ancillary functions such as reabsorption of water. Salivary glands secrete digestive enzymes or merely lubricating fluids. A digestive gland, paired or single, opening into the region between stomach and intestine, commonly supplies the principal digestive juices. In certain invertebrates, as in the crayfish and starfish, such glandular diverticula are also the chief sites of digestion and absorption. Unicellular glands which secrete lubricants or enzymes may also occur throughout the lining of the digestive tract. As in the vertebrate, absorption involves the passage of the products of digestion through the lining of the tract into any blood or lymph spaces in its wall, or directly into the fluid of the body cavity. The parallel with structure and function in the vertebrates is obvious, and it is clear that the same fundamental mechanisms operate in the digestive systems of all animals possessing a complete digestive tract with mouth and anus.

Circulatory Systems. The circulatory systems of invertebrates are very diverse. In the protozoans cyclotic movements of the cytoplasm often transport food vacuoles and absorbed nutrients throughout the cytoplasm, performing a function which corresponds to that of the circulatory systems of metazoans. Another analogous but fundamentally dissimilar mechanism is found in sponges, where currents of water passing through the body furnish a transportation system for food and for excreta. In Coelenterata and Ctenophora, the need for a vascular transport system is obviated by the close relationship existing between the digestive cavity and all other parts of the body. No parts are far removed from the cavity itself, or from its branching extensions in some forms. By muscular contractions, or by flagellary currents in the enteron, food and products of digestion are circulated through the entire body, and the enteron is therefore sometimes called a **gastrovascular cavity**. Among bilateral forms Platyhelminthes present a similar relationship: there is no anus, and the highly branched enteron, when present, commonly extends throughout the body. A circulatory function is often attributed to the lympth-like fluid which fills the interstices of the mesenchymal mass surrounding the organs. In Nemertinea, which have a complete digestive tract, there are blood vessels, although they form a very simple vascular system without a localized propulsive mechanism and without a definitely directed circulation (pp. 340–343).

The more efficient blood vascular systems of higher invertebrates are characteristically provided with some mechanism which propels the blood along a definite circulatory pathway. The simplest of these involves peristaltic contractions of the principal blood vessels. This may be illustrated specifically by the circulatory system of an annelid, such as the earthworm (pp. 406–407); here the larger vessels are contractile and so drive the blood through the body in a definite course. The so-called "hearts" of the earthworm are merely enlarged vessels connecting the dorsal and ventral parts of the system.

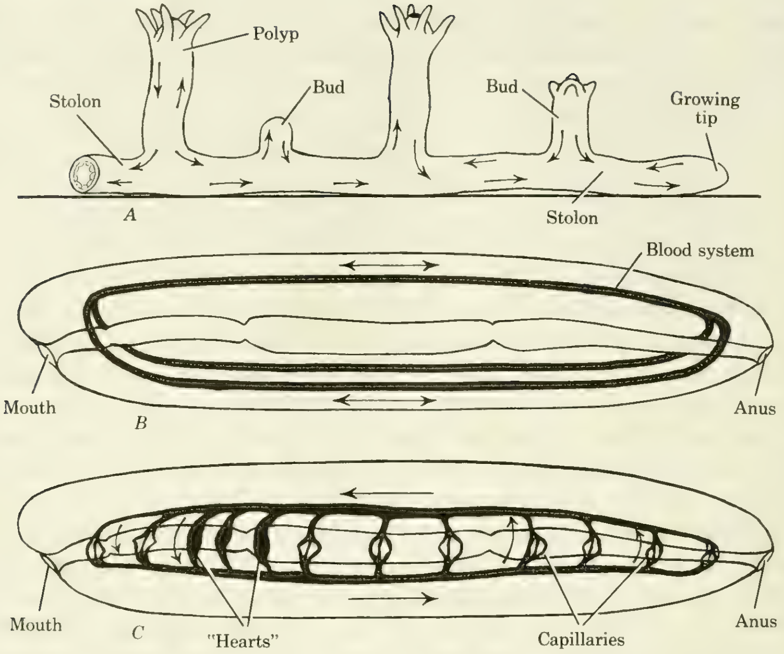


Fig. 17.2. Schematic diagrams of circulatory mechanisms in invertebrates. *A*, circulation within a coelenteron, extending to all parts of the body (Coelenterata). *B*, blood vessels without pulsatile walls, the blood being driven back and forth by movements of the body (Nemertinea). *C*, blood vessels extensively developed, the larger ones being pulsatile and maintaining a definite circulatory course of the blood (Annelida).

The true **heart**, which is found in all well-developed circulatory systems, probably arose in evolution through localization and specialization of the contractile functions of a major blood vessel.

Among well-developed invertebrate circulatory systems, two major types can be distinguished. In one, called the **closed system**, the blood is enclosed within vessels that are continuous through a circuit of heart, arteries, capillaries, and veins. Such a system is found in many annelids, and in cephalopod mollusks such as the squid (see Fig. 13.19, p. 391). More common among invertebrates is the second type, the so-called **open system**, exemplified in pelecypod mollusks (see Fig. 13.3, p. 374). In these animals blood flows from the heart through arteries to all parts of the body; leaving the smallest branches of the arteries, it passes not into capillaries but into intercellular spaces of the mesh-like mesenchymal tissue, collectively called **sinuses**. From these sinuses blood enters the smallest branches of the veins and so is returned to the heart.

Arthropods such as the crayfish have a similarly open system, in which the sinuses form large perivisceral cavities constituting the **hemocoel**. Such a system, unlike that of pelecypod mollusks, lacks veins; arteries extend from the heart to all parts, and from these blood percolates through the tissues into the hemocoel. Return to the heart involves certain tubular specializations of the hemocoel, plus the pericardial sinus. In insects the system is even simpler, because there are no arteries, although the anterior extension of the heart may be termed an aorta. A unique feature of the arthropod system is the manner in which the pericardial chamber has become a part of the hemocoel; blood enters the heart from this cavity through small openings in the heart wall termed **ostia**. These admit blood to the heart during the diastolic phase of its beat, and the backflow of blood during systole is prevented by the action of valve-like flaps covering the ostia. In pelecypod mollusks the pericardial cavity is not involved in the circulatory function; present in the ventricle wall are ostia through which blood enters from a pair of auricles or atria which are a part of the venous system. In some tracheate or air-breathing arthropods the circulation through the hemocoel is aided by dorsal and ventral perforated membranes, termed diaphragms,

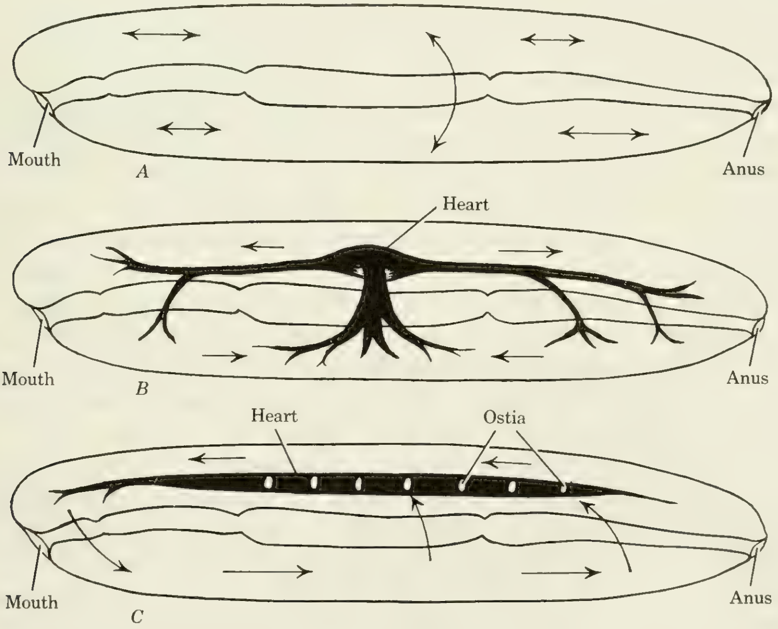


Fig. 17.3. Invertebrate circulatory mechanisms, continued. *A*, the function of transport served by fluid in the pseudocoel, circulated by movements of the body (Aschelminthes). *B*, an "open" circulatory system in which a pulsatile ventricle and distributing vessels conduct blood to the tissues, where it flows into sinuses; blood is returned to the ventricle through vein-like channels and a pair of auricles or atria (pelecypod mollusks). *C*, an open system with a tubular heart bearing lateral ostia through which blood enters the heart; blood flows anteriorly into the intercellular spaces of the hemocoel, eventually returning to the heart (Insecta).

which apparently function in directing the flow of blood through the body spaces. It will be recalled that in these tracheate forms the blood has no oxygen-carrying capacity, this function being performed by the branching tracheal tubules.

Examples of well-developed and representative circulatory systems among the invertebrates are thus found in the Annelida, the Mollusca, and the Arthropoda; the fundamental functional requirements are met in these groups by related though dissimilar structural specializations. The effective circulatory mechanism of most echinoderms is unique, involving the coelomic fluid which is kept in motion by the flagellated peritoneum. Among echinoderms only holothurians and echinoids have a blood-vascular system, the haemal system, retaining a residual circulatory function. In other phyla of invertebrates circulatory systems are absent or but slightly developed. Except for certain invertebrates, such as the tracheate arthropods, general functions of the circulatory system are similar wherever such a system exists, whether in vertebrates or in invertebrates. The circulating fluid brings nutrients, oxygen, and in many instances hormones, to the tissues and carries away for disposal the gaseous and nitrogenous waste products of metabolism. Various circulatory mechanisms are shown schematically in Figures 17.2 and 17.3.

Respiratory Systems. Typical animals must continuously exchange oxygen and carbon dioxide with their environments. Special organs to serve this function are not commonly found among invertebrates in which gas exchange can be carried out over a large part of the body surface, as in the hydra and the earthworm. Generally speaking, development of such special structures occurs concomitantly with increase in size and thickness of the body. This generalization follows the well-known fact that large bodies have much less surface area per unit of volume than smaller bodies. The flattened, leaf-like body form in the relatively large platyhelminth worms may be interpreted as an adaptation that compensates for the lack of special respiratory organs by decreasing the thickness of the body. Among invertebrates that have developed organs for respiration, the apparently diverse mechanisms can be classified into a few general types, schematically represented in Figure 17.4. These structures are without exception related to the environmental situation in which the animal lives, although they are often conditioned by the ancestral history of the animal. Primarily aquatic species are commonly provided with **blood gills**, which are outgrowths of the surface of the body with a particularly copious blood supply. These may be external gills, as in the branchial filaments and parapodia of polychaete annelids (pp. 398–402); or, as in pelecypod mollusks and the larger crustacea, they may be enclosed within a cavity opening at the surface. Many echinoderms have dermal branchiae or other thin-walled outpocketings of the body wall through which respiratory exchange occurs between coelomic fluid and external sea water. Holothurians, again, are unusual in their possession of the "water lungs," which are functionally analogous but certainly not homologous with the respiratory organs of other echinoderms. Only rarely do terrestrial animals. possess blood gills, and those that do, like terrestrial isopod crustaceans, are strictly limited to very moist environments.

Adaptation to the typically dry conditions of life on land has involved the development of either **lungs** of various kinds or of **tracheal systems.** The lungs of pulmonate gastropod mollusks are modifications of the mantle cavity and its lining; and the "book lungs" of spiders suggest the plate-like gills of some aquatic chelicerates, withdrawn within a protected cavity. The tracheal systems of terrestrial arthropods such as insects consist of air tubes through which atmospheric air is brought into the body. It may be recalled that readaptation to an aquatic environment has occurred among both pulmonate gastropods and tracheate arthropods, but never has there been a return to the blood-gill system. Adult forms continue to use atmospheric air, but aquatic immature stages of insects often develop tracheal gills.

The functional relationships are similar in all these adaptations; a thin layer of cells separates the blood or body fluid of the animal from the external water or air that is the source of oxygen for the animal. The site at which oxygen is gained by the blood is also the site at which carbon dioxide is eliminated from the body, whether it be over the general body surface, at gills, in lungs, or in tracheae. Thus it is clear that there is no discontinuity in these functions betwen invertebrates and vertebrates, which also possess gills or lungs. As previously indicated the processes of **cellular metabolism** are also fundamentally similar throughout the animal kingdom; oxygen is utilized within the cells in enzymatically controlled, sequential reactions involved in the transformations of energy which are the basis of all metabolism (see pp. 35–38). There are special cases of animals, notably intestinal parasites, inhabiting environments in which free oxygen is unavailable or present in very low concentration. The metabolism of these forms chiefly involves only the anaerobic phase.

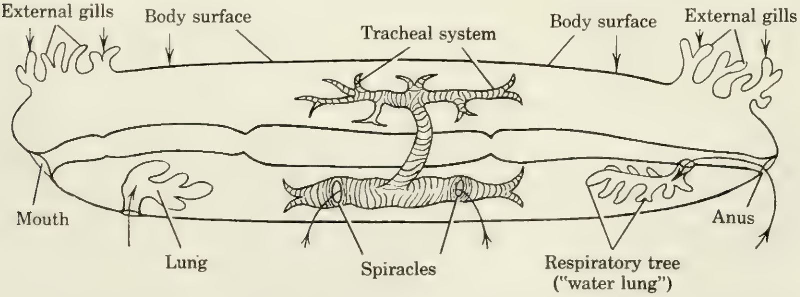


Fig. 17.4. Schematic diagram representing a composite of many mechanisms of gaseous exchange found among various invertebrate animals.

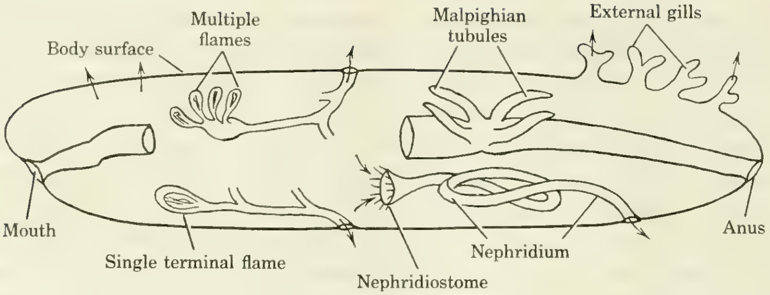


Fig. 17.5. Schematic diagram representing a composite of many excretory mechanisms in invertebrate animals.

Excretory Systems. As a result of metabolic processes, the cells of all animals are constantly producing waste substances. One of the chief by-products of cellular oxidation is carbon dioxide, and the metabolism of proteins and amino acids results in the formation of various nitrogenous wastes as by-products. Carbon dioxide and nitrogenous wastes are generally of no further use to the animal, and continued accumulation of these substances would poison the body. Therefore, one of the problems of animal existence is the elimination of these wastes. As we have seen, important functions of the circulatory system involve the transport of excreta from the tissues to specialized sites of elimination. Carbon dioxide is commonly lost to the external environment in the respiratory process, but the removal of nitrogenous wastes poses special problems which have been solved in different animal groups in diverse ways. Like the respiratory mechanisms, these excretory devices are markedly influenced by environmental factors, conditioned by the evolutionary history of the animal and its level of organization. Various excretory mechanisms of invertebrates are shown schematically in Figure 17.5.

Microscopic and moderately small animals, such as Protozoa, Porifera, Coelenterata, and Ctenophora, have no specialized excretory organs. In these forms the area of body surface exposed to the external environment is very extensive, and excreta are eliminated by diffusion. In some protozoans we have seen how contractile vacuoles may be involved in the excretory processes, although their primary function is to maintain the water balance of the organism. In some of the simpler metazoans, such as the radiate phyla, aggregations of cells have been described in which crystalline deposits of nitrogenous substances are stored. These cells may perform an excretory function in isolating complex nitrogenous wastes, but it has been demonstrated that the principal excretory product in all these animals is ammonia, which is highly soluble and easily eliminated by diffusion from small bodies.

Most bilateral forms have developed organs of one type or another which are classically interpreted as excretory. Among these are **protonephridia**, or flame-bulb systems; **nephridia** (including **metanephridia**), which generally possess ciliated coelomic funnels; and **Malpighian tubules.** Protonephridial systems are commonest among acoelomate and pseudocoelomate Bilateria; they occur in practically all Platyhelminthes, in many Aschelminthes, in Entoprocta, and others; but they are also found in eucoelomate forms, in the larval stages of many mollusks, in annelids, and even among the invertebrate chordates such as *Branchiostoma.* With such a wide phylogenetic distribution, protonephridial systems exhibit great variability. The chief unifying feature is the presence of **flame bulbs,** but these may consist of individual cells with single tufts of cilia, groups of cells with numerous ciliary "flames," or single or grouped cells each bearing a single, long flagellum beating in a tube; this last type is generally termed a **solenocyte** (Fig. 17.6). A primary excretory function has never been conclusively demonstrated for protonephridial systems. The evidence indicates rather that they are involved in maintenance of the water balance of the organism. However, like protozoan contractile vacuoles, it is likely that in eliminating excess water they also flush out wastes in solution.

Nephridial or metanephridial systems are characteristic of many types of eucoelomate animals. Morphologically, the systems vary considerably from one phylum to another, but they usually exhibit as a common feature ducts with funnels opening into the coelomic cavity or its derivatives. In pelecypod mollusks, for example, there is a single pair of these organs, and the funnels open into the pericardial coelom. In such annelids as the clamworm and the common earthworm, there is a pair of nephridia with individual ducts and external nephridiopores for each of the segmental coelomic cavities (Fig. 17.5). In chelicerate and crustacean arthropods, where the coelom has been largely replaced by a hemocoel, the excretory organs (coxal glands and green glands, respectively) are interpreted as remnants of a primitive series of paired nephridial organs; the internal end sac of the crustacean green gland is thought to be a vestige of the ancestral coelomic cavity (see Fig. 15.6, p. 433). The assignment of excretory functions to nephridial systems rests on firm experimental evidence, although details of the processes involved are unknown for many types. In mollusks and annelids the excretory organs are associated not only with the coelomic fluid but also with specific blood vessels. The functions of these organs, in those annelids in which they have been especially studied, appear to involve an initial passage of wastes from the coelomic fluid, followed by selective reabsorption of salts into the blood in the specific vessels associated with the tubular parts of the organs. In crustaceans the functions of the green glands and the nature of the urine, whether concentrated or dilute, appear to be correlated with the environment of the animal. In the fresh-water crayfish, for example, with well-developed tubules, the salt content of the urine is less than that of the blood; the tubules appear to extract salts from the urine, returning them to the blood. In the lobster, however, the urine has the same salt concentration as the blood; it is not modified in passing through the tubular parts, which are very

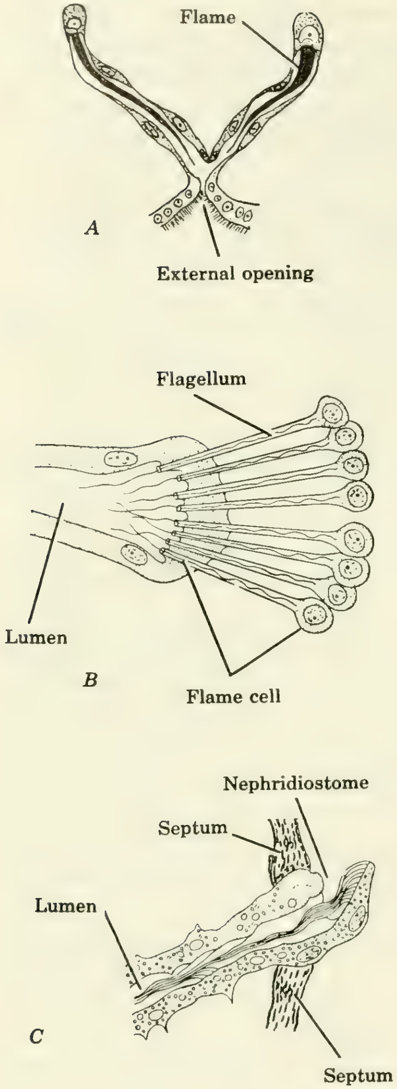


Fig. 17.6. Some excretory mechanisms in invertebrates. *A*, protonephridial system of *Pedicellina*, an entoproct (pp. 356–357). *B*, portion of a solenocytic protonephridial unit of the polychaete annelid *Phyllodoce*, shown in section. *C*, nephridiostome of a nephridium in another polychaete, *Trypanosyllis;* note the arrangement of cilia in the open funnel and proximal parts of the tubule (cf. nephridium of *Lumbricus*, Fig. 14.9, p. 408). (*A*, from C. Cori in W. Kükenthal and T. Krumbach, 1933, *Handbuch der Zoologie; B* and *C*, from C. G. Rogers, *Textbook of Comparative Physiology*, copyright 1938 by McGraw-Hill Book Co., Inc., reprinted by permission.)

much reduced. In an apparently entirely different environmental situation, but one governed by the same need to conserve water as that facing marine animals, some species of earthworms adapted to dry terrestrial conditions have been found with nephridial systems unlike those of the common forms. In these specialized annelids, the nephridia open not on the surface of the body but into the digestive tract, where active reabsorption of water occurs through the intestinal wall into the blood.

Malpighian tubules, developed in most terrestrial arthropods, apparently represent an analogous adaptation for water conservation. Nitrogenous wastes are collected from the hemocoelic blood into the tubules, where they are concentrated by reabsorption of water and passed into the hind-gut (see Fig. 15.19, p. 450). Here further amounts of water are extracted, and the residue is finally eliminated from the body as a relatively dry, crystalline mass.

Still another mechanism for the removal of wastes from the body fluids is widely distributed among invertebrates, appearing in many forms as the only excretory pathway other than simple diffusion, and in others as an accessory to one of the systems just discussed. This involves the activities of numerous fixed or amoeboid cells, of mesodermal origin, which accumulate wastes from the blood or coelomic fluid and store them as granules or spherules within their cytoplasm. This storage may be temporary or permanent. In echinoderms amoeboid cells of the coelomic fluid accumulate wastes and engulf foreign particles, and the cells containing these accumulations are eliminated from the body by passing through the walls of the dermal branchiae or "water lungs" into the sea water. Cells in other locations appear to store isolated wastes throughout the life of the echinoderm. In insects the cells of the fat body and other tissues function similarly in the accumulation of wastes; this is particularly notable during the pupal stage, when elimination of nitrogenous excreta from the body is impossible. The activities of all these waste-storing cells, known generally as **athrocytes**, help prevent wastes from reaching toxic concentrations in the body fluids. From the functional standpoint it is not necessary that the wastes be completely eliminated from the body; they can be as effectively isolated by sequestration in certain cells where they are held in "dead storage."

Broadly comparative studies make it clear that the nephridial excretory systems of eucoelomate invertebrates have developed primarily in connection with the coelomic cavities, and it is probable that their original functions involved the elimination of nitrogenous wastes dissolved in the coelomic fluid. In many of these forms a copious blood supply to the nephridia has been established through the vascular system, indicating a possible shift of the pathway of excretion from the coelomic fluid to the cirulating blood. A parallel development of excretory mechanisms occurs in the vertebrate phylogenetic series and in the ontogeny of the higher vertebrates. Here the earliest excretory organs develop in connection with the coelom, which they drain through ciliated funnels; these primitive relationships are subsequently replaced by vascular connections, which make possible the extraction of wastes from the circulating blood.

Systems Related to Responsiveness and Integration

One of the characteristics of living things is **responsiveness**, the capacity to react to changes in the environment. The behavior of such simple animals as the amoeba is based on, and limited by, the inherent reactivity or responsiveness of the single cell. Such primitive behavior patterns would not suffice, however, for more complex animals leading more active lives. Even among higher protozoans, as in *Paramecium*, protoplasmic organelles have developed to serve in coordinating the activities of different parts of the unicellular body. The problem of adequate integration is more acute in multicellular forms, which are generally much larger. Here an environmental change or stimulus acting upon some part of the body must be reacted to by the body as a whole, or by some part distant from the point of stimulation; and the reaction may commonly involve thousands of cells. As we have seen, in most metazoans, special cells, tissues, and organs, culminating in what may be termed **sensory-neuro-motor systems**, have evolved as integrative mechanisms. These represent devices by which animals rapidly perceive environmental changes, and by which appropriate responses are quickly set in motion.

In Chapter 4, an account was presented of another type of coordinating mechanism as it appears in vertebrates, involving **endocrine organs** and their secretions, the **hormones**. For the most part, these are adapted to slow, long-term integration of bodily changes, such as regulation of growth, control of metabolic rates, cyclic maturation of gonads and gametes, and so on. It was long supposed that this **chemical coordination** was limited to vertebrates, but a steadily growing body of information makes it clear that analogous mechanisms operate in a wide variety of invertebrates as well. Here we shall present a brief survey of the general features of these dual integrative systems, nervous and chemical, as they occur in some typical invertebrates.

Sensory-neuro-motor Systems. The behavior of protozoans reveals that they respond to environmental changes in predictable ways. Particularly among ciliates (pp. 250–253), it is possible to find, in the sensory cilia, the conductile fibrillar systems, and the contractile motor organelles, intracellular structures which parallel the mechanisms for reception, conduction, and response in multicellular forms.

In the Porifera the only normal reactions to stimuli appear to involve the closing of pores and oscula, contractions of the entire sponge, and adjustment of the diameters of parts of the canal systems. The **effectors** for these activities are simple, spindle-shaped muscle cells arranged about openings and canals. These were long believed to be **independent effectors**, but the recent discovery of typical though primitive nervous elements in sponges makes it appear that these organisms possess well-developed **receptor-effector** mechanisms of coordination. Neurons apparently conduct impulses from choanocytes and from simple surface receptors to the muscle cells and mediate coordinated activities of a simple kind throughout the body of the sponge (Fig. 17.7).

The nervous system of coelenterates is of the type described for the hydra (pp. 293–297). Sensory cells and neurosensory cells are the **receptors**; specialized nerve cells perform the function of **conduction**; and the contractile processes of the large epitheliomuscular cells are **effectors**. These relationships

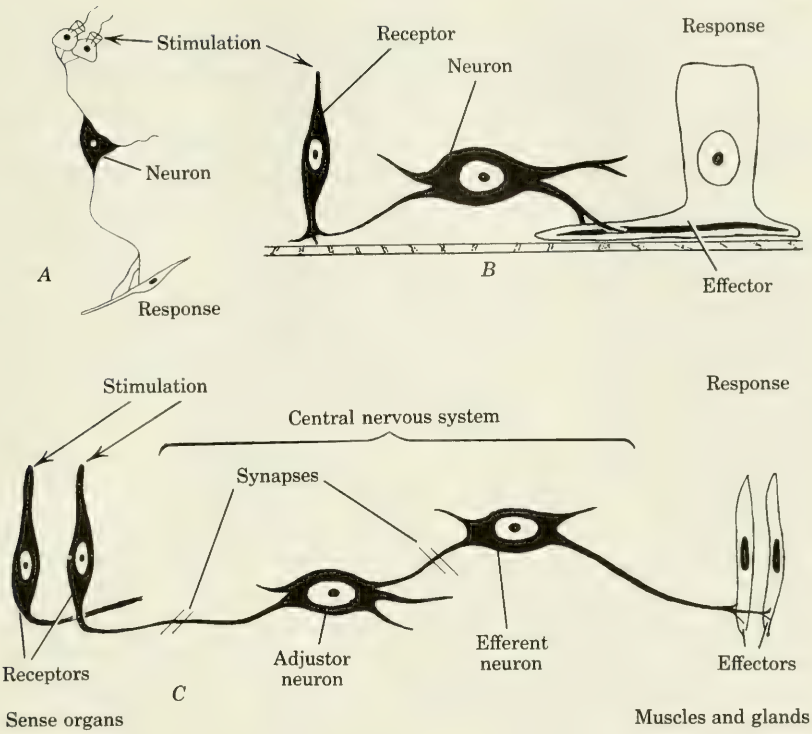

Stimulation
Receptor
Response
Neuron
Neuron
A
B
Response
Effector
Stimulation
Response
Central nervous system
Synapses
Receptors
C
Adjustor neuron
Efferent neuron
Effectors
Sense organs
Muscles and glands

Fig. 17.7. Mechanisms of nervous integration among invertebrates; diagrammatic. *A*, receptor-effector system of a calcareous sponge. *B*, receptor-effector system of Coelenterata. *C*, receptor-adjustor-effector system, as in Annelida and all the more complex invertebrates. (*A*, redrawn from O. Tuzet, R. Loubatieres, and M. Pavans de Ceccaty, 1952, *Comptes rendus de l'Académie des Sciences*, vol. 234.)

are shown schematically in Figure 17.7. The interconnections between the cellular elements in this system seem to be synaptic, as in higher forms, rather than continuous protoplasmic bridges, as was once believed. The nematocysts appear to function as **independent effectors.** In many jellyfishes there are quite well-developed **sense organs,** such as the eyes and organs of equilibration. No concentrations of nerve cell bodies to form **ganglia** occur in coelenterates, however, and there are no functional indications of the presence of a central nervous system, with adjustment of impulses and directed reflex activity. The nervous system of coelenterates may be characterized, therefore, as a **receptor-effector** system, corresponding functionally to that of sponges but more highly organized.

The nervous system of annelids is representative in general of that found in most higher invertebrates. Specifically, as in the earthworm, the **receptor** elements are neurosensory cells in the epidermis. Each of these cells has a principal process or axon, extending as a nerve fiber which enters the ventral nerve cord; lesser processes of these cells may connect with the nerve cells of a **subepidermal nerve net** or **plexus.** Within the nerve cord the fibers of the neurosensory cells may make synaptic contact directly with **efferent neurons;** or their synapses may be with cells called **adjustor** or **association neurons,** whose chief function is the distribution of incoming impulses among many efferent neurons. The branching processes of adjustor neurons lie entirely within the nerve cord, but the principal fibers or axons of efferent neurons pass outward from the cord to make contact with muscle cells or other effectors, as shown diagrammatically in Figure 17.7. The resemblance of this type of system to that found in vertebrates is apparent. Like the vertebrate nervous system, the sensory-neuro-motor mechanism of the annelid consists of two interconnected divisions, the **central system,** the "brain" and the nerve cord, and the **peripheral system,** the nerves and their component nerve fibers. The relationship to these divisions of the neurosensory cells and sense organs, and of the muscles and glands which are the effectors, is similar in the annelid and in the vertebrate.

In the annelid, stimulation of peripheral neurosensory cells sets up **nerve impulses** which travel to the subepidermal plexus and also along the axons of the sensory cells extending into the ventral nerve cord. Within the nerve net the impulses seem to pass in all directions from their point of origin, as in the coelenterate nerve net, but not for any great distance. Within the nerve cord the pathway of impulses may be a short cut to an efferent neuron and thence outward to a nearby effector; or it may involve the mediation of one or more adjustor neurons and so extend to any part of the animal. In addition to the more typical adjustor neurons, the nerve cord of the annelid contains what are called **giant fibers;** these function for the rapid conduction of impulses over long distances within the cord.

Like the vertebrate nervous system, that of the annelid is a **receptor-adjustor-effector system.** The differences between the two systems lie not in fundamental relationships of parts but in degree of complexity. In the vertebrate there are more adjustor or association neurons, and hence more complicated connections and pathways within the central nervous system. The complexity is notably greater in the vertebrate brain, a region which is relatively much larger in the vertebrate than in the annelid, and in which the number of nerve pathways is infinitely multiplied. The brain of the vertebrate is also the region which is most intimately related to the highly specialized sense organs of the head. Similarly, in the annelid, the concentration of ganglion cells in the anterior end, forming the so-called "brain," lies close to, and mediates the functions of, the most sensitive parts of the earthworm and the specialized eyes and antennae of the clamworm and other polychaetes.

The main advances of the annelid type of nervous system over that of the coelenterates involve two interrelated lines of specialization: the concentration of ganglion cells to form a central nervous system, and the development of adjustor neurons within the central system to mediate impulses between afferent and efferent neurons. These advances made possible the development of one-way conduction and of reflex circuits, in place of the diffuse nerve pathways characteristic of the net-like system of sponges and coelenterates. The subepidermal plexus of annelids, a minor part of the nervous system, is similar in structure and function to the nerve net of coelenterates. The brain of the annelid may be interpreted as an adaptation to its active, progressive way of life, correlated with the development of sense organs in the anterior region of the body.

In Mollusca and Arthropoda the nervous system is a receptor-adjustor-effector mechanism essentially like that of annelids. Active and highly evolved forms, such as squids among mollusks and many insects and spiders among arthropods, have specialized sense organs and effectors of great complexity, and the adjustor mechanisms are correspondingly complicated. In the squid, particularly, large areas of the brain are given over to purely associative functions. The same situation exists in connection with the mechanisms of nervous coordination in vertebrates. Thus, from the earthworm to man the differences consist in the increased number and specialization of receptors, adjustors, and effectors, not in changes of basic cellular relationships. It is very interesting to realize that, in invertebrates as well as vertebrates, the passage of a nerve impulse from one neuron to another, or to a motor end organ, appears commonly to involve the liberation of a chemical mediator. This secretion, if released in adequate quantities within a sufficiently short period of time, stimulates the second neuron or the effector; the mediator is prevented from exerting its effect continuously by the presence of a specific enzyme which brings about the immediate destruction of the mediator. There are several known substances capable of thus controlling the spread of nervous excitation, and some are common to both vertebrates and invertebrates (see p. 113).

Endocrine Mechanisms. In addition to nervous integration, many invertebrates have evolved mechanisms of chemical coordination analogous to those of vertebrates. Such mechanisms are best known among Arthropoda. In crustaceans they are involved in control of integumental color changes and of molting, and in insects they regulate growth, differentiation, and metamorphosis (p. 456). Other hormonal effects, suspected but less definitely established, appear to operate in the expression of sex, in the maintenance of blood-sugar levels, and in the general control of metabolic rates. The endocrine organs of invertebrates are composed largely of **neurosecretory cells**, which appear to be nerve cells modified to perform special secretory functions (Fig. 17.8). As recalled above, the passage of a nerve impulse from one neuron to another appears always to involve the secretion of a chemical mediator, and to this extent all neurons are neurosecretory cells. However, the secretions of the specialized endocrine cells of invertebrates are not the same as those involved in the stimulation of adjacent neurons or effectors. Hormones may pass by way of nerves, or they may be released into the blood or body fluids and exert their characteristic effects on other organs or tissues distant from the source of the hormone.

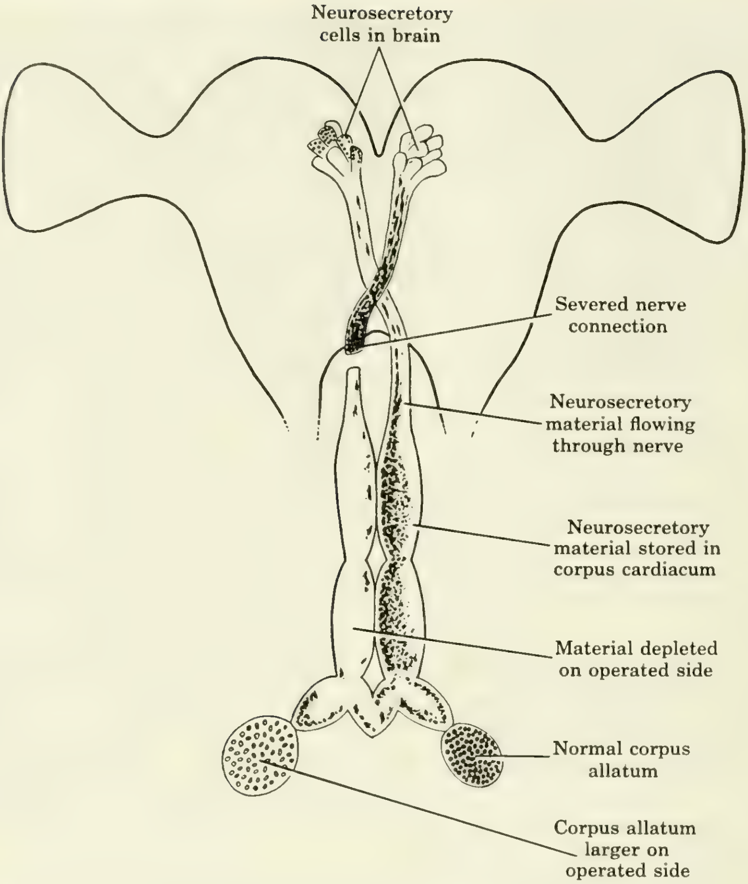

Neurosecretory cells in brain
Severed nerve connection
Neurosecretory material flowing through nerve
Neurosecretory material stored in corpus cardiacum
Material depleted on operated side
Normal corpus allatum
Corpus allatum larger on operated side

Fig. 17.8. Neurosecretory function in an insect, *Leucophaea maderae.* The material produced in the cerebral neurosecretory cells normally flows posteriorly through nervous connections into a storage organ, the corpus cardiacum, and exerts an effect on a pair of endocrine organs, the corpora allata. If the nervous connection between brain and corpus cardiacum is severed, neurosecretory products accumulate at the point of section, the material stored in the corpus cardiacum is depleted, and changes occur in the function of the corpus allatum. (Adapted from B. Scharrer, 1952, *Biological Bulletin*, vol. 102, printed by permission.)

In the best-known examples, among arthropods, different groups of neurosecretory cells form functional endocrine systems. Some environmental or physiological change causes the release of a hormone by one gland, and this hormone has the specific effect of stimulating another gland to produce its secretion, which in turn exerts its systemic or specific effect. In many invertebrates the relationships are complex, just as they are in mammalian endocrine systems (pp. 117–124). It is well known that among mammals the hormones are generally not "species specific" in their action; hormones used for the treatment of human endocrine insufficiencies are obtained from sheep and cattle, as by-products of slaughter-house operations. This same lack of specificity is characteristic, within limits, of many endocrine systems among invertebrates. Extracts, or entire glands, from one species of crustacean will exert their usual effect when appropriately administered to other kinds of crustaceans. It has recently been announced that from several thousands of silkworms a minute amount of a purified, crystalline substance has been prepared which represents the "growth and differentiation hormone" of this species, produced in the prothoracic glands (pp. 456–457). It is a relatively simple organic compound with the empirical formula $C_{18}H_{30}O_4$. It is very powerful in its action and is effective in initiating metamorphic changes in several insects other than the silkworm. The "juvenile hormone" produced in the corpus allatum has also been identified in extracts of certain insects and will probably soon be isolated.

In contrast to the typical invertebrate endocrine system as now understood, endocrine organs in vertebrates do not as a rule involve neurosecretory cells. An exception to this statement is provided by the posterior lobe of the pituitary gland in mammals. This organ appears to act chiefly as a reservoir for hormones produced by neurosecretory cells in the part of the brain to which it is attached. It is noteworthy that in both vertebrates and invertebrates modified neurons have become adapted as endocrine organs, thus furnishing a physical as well as a functional relationship between the dual mechanisms of coordination, nervous and chemical.

Supporting Mechanisms: the Skeleton

The skeletons of animals furnish support for the body and serve as places of attachment for muscles, which for effective action must have a firm anchorage. To a varying degree, certain kinds of skeletons may also function in enclosing and protecting the soft parts of the animal; and some superficial structures related to skeletons seem principally adapted only to this last function. Skeletons may usually be classified in two general types, **exoskeletons** and **endoskeletons**. Exoskeletons typically cover the surface of the body, contain no cells, and are secreted by the underlying epidermis. In contrast, endoskeletons usually lie deeper within the body, enclose cells which produce the skeletal material, and are of mesodermal origin. In some animals exoskeletons become embedded in the superficial tissues of the body, and in others endoskeletons appear to lie at the surface, so that position alone is not a reliable criterion. The majority of skeletons among invertebrates are exoskeletons, but there are many examples of endoskeletons also.

Even among Protozoa, supporting and protective structures have been developed that parallel the two types of metazoan skeletons. Many Sarcodina, such as *Arcella*, radiolarians, and foraminiferans, lay down protective coverings and supporting skeletons of organic or various inorganic materials.

The rod-like bodies related to the locomotor apparatus in some flagellates, formed within the cell, seem to function also as supporting skeletal structures.

The vast majority of sponges produce some kind of supporting framework. In calcareous and siliceous sponges, this may consist of individual spicules of calcium carbonate or of glass, or these spicules may be fused into a continuous latticework. The Keratosa produce skeletons consisting of interlaced fibers of the proteinaceous substance termed **spongin**. All these skeletal elements are synthesized by individual mesenchyme cells called **scleroblasts** and first appear as intracellular crystals or fibers (see Fig. 9.9, p. 277). In the finished condition they may be enclosed within the mass of the sponge or lie at the surface, so that a distinction between endo- and exoskeletons in the Porifera is impossible.

Among the simplest eumetazoans, which, unlike sponges, have evolved true tissues, supporting structures are widespread and varied. Coelenterates like *Hydra* and jellyfishes possess no skeletons, the function of support being served by the mesolamella or the turgid mesogloea. Colonial hydrozoans, with the exception of siphonophores, commonly form tubular exoskeletons known as the **perisarc**, as in *Obelia*. Anthozoans either have no skeletons, as in *Metridium* and other sea anemones, or produce protective and supporting structures varying from the calcareous, epidermal secretions of corals to the organic skeletons of sea fans and similar forms. Inasmuch as these latter skeletal elements lie deeply embedded in the body and seem to be of mesodermal origin, they may be considered endoskeletal.

Among Platyhelminthes true exoskeletons are lacking, although protective cuticular coverings are common in parasitic forms. It should be noted, however, that these organic covering layers are not homologous with the epidermally produced cuticles and exoskeletons of higher forms. In adult trematodes and cestodes the epidermis is lacking, and the cuticle is secreted by underlying mesenchymal cells.

A common pattern of skeleton formation appears throughout the pseudocoelomate and schizocoelous eucoelomate groups. The basic "skeleton" is a cuticular covering, organic in nature, secreted by epidermal cells. This type of protective covering is typical of all Aschelminthes and of annelid worms. The skeletons of brachiopods, ectoprocts, and mollusks appear to be modifications of this basic cuticle, commonly made more effective by the deposition of layers of calcium carbonate within and beneath the organic material. It will be recalled that the shells of bivalves, for example, are covered by an organic **periostracum**. Some cephalopod mollusks present interesting advances correlated with their more active mode of life, in which a bulky calcareous shell would be a handicap. The squid retains a remnant of the ancestral exoskeleton, an organic, axial supporting structure called the "pen," which has become so surrounded by the tissues of the mantle as to resemble an endoskeleton. This animal has developed true endoskeletal elements, however, in the head region; there is an internal cartilaginous structure which serves to protect the brain and eyes and to anchor the muscles of the jaws and arms.

It bears a striking resemblance to the cartilaginous "chondrocranium" of the vertebrate series.

The arthropod exoskeleton appears to be a different modification of the basic cuticle, which has been thickened and stiffened by additional deposition of organic materials, such as scleroproteins and chitin. In some of the larger aquatic crustaceans, calcium salts have also been added to the skeleton. The most significant skeletal advance among arthropods is the breaking up of the exoskeleton into stiff, inflexible portions termed **sclerites**, interconnected by thin, flexible joints. Many parts of the arthropod exoskeleton have become folded inward to serve more efficiently as points of muscle attachment. Although these may appear as endoskeletal structures, their origin and nature are clearly like those of the outer exoskeleton. The effect of the development of the rigid and unyielding exoskeleton on growth in the arthropods has been noted (p. 484); mollusks and other enclosed forms grow by the addition of material, continually enlarging the skeleton, but arthropods must shed the exoskeleton and secrete a new and larger one to provide for increase in size. Periodic molting of the cuticular skeleton is also characteristic of the growing stages of Nematoda (p. 352).

The skeletal structures of echinoderms are components of the body wall and thus resemble exoskeletons. These structures are always produced by tissues of mesodermal origin, however, as are the bones of vertebrates, and are covered externally by epidermis. This epidermal covering may be eroded away, as on the tips of spines, but this does not alter the fundamental relationships. Sea cucumbers commonly have flexible, apparently unprotected body walls, but closer inspection reveals the presence of microscopic spicules and plates which are clearly homologous with the skeletons of other echinoderms.

Reproductive Systems and Their Functions

All the organs and systems discussed so far function primarily in the maintenance of the **individual animal**—in its nutrition, in the regulation and integration of its various physiological processes, in the support and protection of its organs, and so on. Unlike these, the reproductive system is of no value in the day-to-day activities of the individual; the survival of the animal does not depend on the proper functioning of its reproductive organs. This system is devoted entirely to the maintenance of the **species** and its projection into the future. In the long view, the activities of the individual are all, directly or indirectly, related to the reproductive process. Unless the individual is well nourished and otherwise capable of survival in its environment, it will be unable to produce new generations of its kind. The problem of reproduction involves not only the formation of new individuals but also their production at such a rate, or in such numbers, as to maintain or increase the population of the species, in the face of what might be termed environmental resistance. The reproductive processes developed among the invertebrates are almost infinitely varied, but all of them are understandable as means to these ends.

Mechanisms of reproduction in many of the simpler animals do not involve the development of organs or of systems, being of an **asexual** nature. Asexual reproduction is common among the protozoans and the more primitive metazoans. Rapid increase in protozoan populations occurs by the **fission,** or division, of one mature animal to produce two daughter individuals approximately equal in size. The organelles of the mature animal, as among ciliates, are commonly divided between the daughters, each of which then elaborates the parts which it lacks. Fission in a protozoan requires, of course, but one cell division to produce two individuals where there was originally one. Reproduction by fission also occurs among many of the simpler Metazoa, as in planarians and other turbellarians. Here, however, the activities of many cells are involved in the replacement of missing parts and in the regulation of form in the daughter individuals. Other types of asexual reproduction found in metazoans are **budding,** common among coelenterates, and a somewhat similar process occurring in the proliferative larval stages of digenetic trematodes. In budding, a daughter individual is not produced "all at once," as it were, by division of the parent body, but develops relatively slowly, growing at the expense of the parent until mature enough to become independent. Reproduction in the larval stages of trematodes involves the subdivision of internal masses of cells into smaller clumps, each of which then develops into a complete individual of the succeeding stage. This process might be termed **internal budding;** it is sometimes considered as a process of **polyembryony** (see p. 209), but in trematodes larval reproduction does not immediately follow the production of a zygote. Wherever asexual reproduction occurs among metazoans, it is generally correlated with a marked capacity for regenerative growth. Both the replacement of parts lost through injury and the development of missing parts in a daughter individual are processes involving the activities of undifferentiated, totipotent cells.

Although asexual reproduction is an effective means of rapidly increasing the population, species with exclusively asexual reproduction are rare among animals. The more primitive groups, including Protozoa, have developed methods of **sexual** reproduction in addition to asexual processes, and among most higher invertebrates reproduction is exclusively sexual. New individuals, beginning as **zygotes,** are formed by the union of male and female **gametes** produced usually by different parents; thus the new individual may receive a mixture of the hereditary characteristics of the two parents, and new genetic combinations may be continually produced in the population. The various systems of organs, chambers, and ducts which form the reproductive systems of most metazoans are elaborations of originally simple arrangements for the transport of gametes from the gonads to the exterior. In many invertebrates specializations of the male reproductive system have developed to facilitate

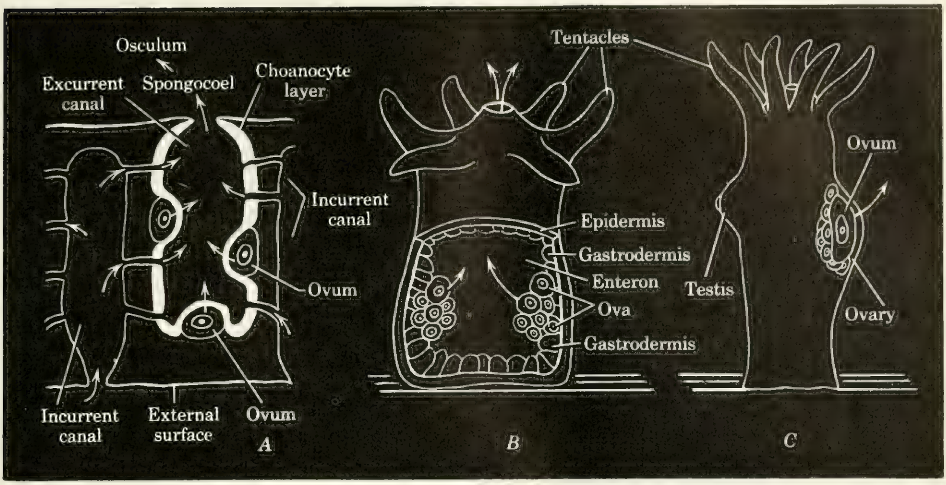


Fig. 17.9. Reproductive mechanisms in some of the simplest invertebrates; schematic. *A*, gametes arise from cells of the mesenchyme-like middle region. Ova are fertilized in place and develop into flagellated larvae, which break through the choanocyte layer into the excurrent canals and are discharged via the spongocoel and osculum (Porifera). *B*, gametes arise from cells of the gastrodermis, are discharged into the coelenteron, and pass to the outside through the mouth-anus (Scyphomedusae and Anthozoa). *C*, gametes arise from interstitial cells of the epidermis and are discharged into the surrounding water (many Hydrozoa).

the introduction of spermatozoa into the body of the female at copulation. In the female special mechanisms are often provided for the storage of sperm received at copulation, for the internal fertilization of ova, for the deposition of protective shells about the resulting zygotes, and in many instances for the retention of zygotes during all or part of the embryonic period. Within any single phylum these reproductive structures are generally homologous in all classes; but when comparisons are made between animals in different phyla, it becomes evident that structures of very diverse origins have become adapted to similar functions in different groups (Figs. 17.9, 17.10).

In keeping with their primitive levels of organization, Mesozoa and Porifera have no reproductive organs or systems, but only reproductive cells which differentiate into gametes. In Coelenterata and Ctenophora reproductive cells become localized in specific, temporary aggregations of cells which are termed "ovaries" and "testes," but these organs are of a very primitive nature, and there are no true reproductive systems. In all these simple groups, with few exceptions, gametes are released into the surrounding water, fertilization is external, and there are few if any provisions for the care and protection of the developing young.

Reproductive systems are of general occurrence among the Bilateria, but it cannot be said without exception that these increase in complexity as

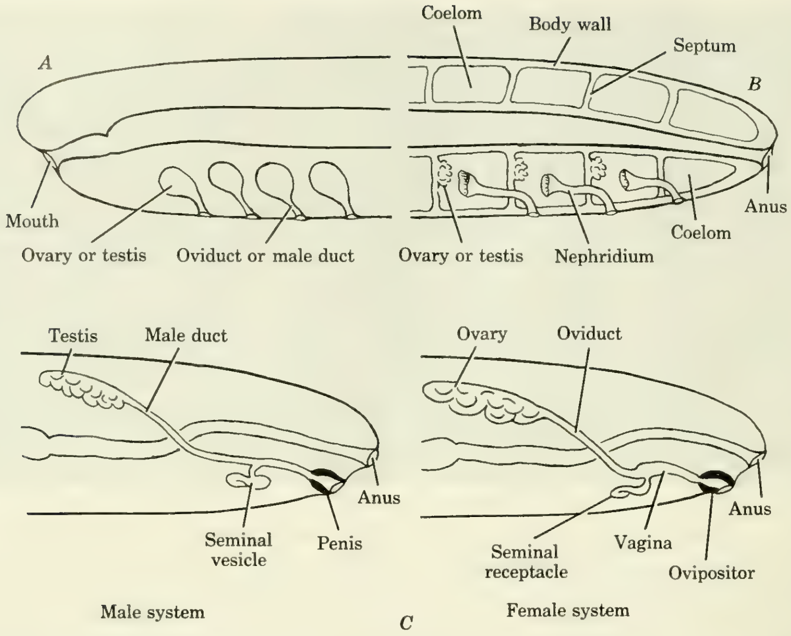

Coelom
Body wall
Septum
A
B
Mouth
Ovary or testis
Oviduct or male duct
Ovary or testis
Nephridium
Coelom
Anus
Testis
Male duct
Anus
Seminal vesicle
Penis
Male system
Ovary
Oviduct
Anus
Seminal receptacle
Vagina
Ovipositor
Female system
C

Fig. 17.10. Reproductive mechanisms in some of the more complex invertebrates; schematic. *A*, gametes mature in individual sac-like gonads and are discharged to the outside, where fertilization and development occur (Nemertinea). *B*, gametes are produced by proliferation of the coelomic lining, or in special chambers derived from the coelom; gametes reach the outside through nephridia or coelomoducts, and fertilization is external (Annelida). *C*, ovaries and testes are not obviously related to the coelom; special structures, such as seminal vesicles, seminal receptacle, penis, and ovipositor, develop in relation to internal fertilization (Insecta).

animals become more complex. In fact, the simplest bilateral animals, the Platyhelminthes, have surprisingly complicated reproductive systems. Beginning with Acoela, whose only organ systems are reproductive systems, turbellarians develop very effective reproductive mechanisms. These include provisions for copulation, internal fertilization, and the deposition of shelled capsules in which the young pass their embryonic stages. Each individual turbellarian commonly possesses both male and female systems, although cross-fertilization appears to be the rule. Thus, the extremely well-developed reproductive systems of the parasitic trematodes and cestodes are foreshadowed in their free-living relatives, and the adaptations for parasitic life involve chiefly differences in degree, not in fundamental organization. In contrast to the Platyhelminthes, the Nemertinea, of the same general grade of organization, have very simple reproductive organs, consisting of series of pouch-like ovaries or testes, each with its individual external opening.

In pseudocoelomate animals the gonads lie in the pseudocoel and connect directly with reproductive ducts. Ova are fertilized internally, and zygotes are usually encased in protective shells before being passed to the outside. In many pseudocoelomates, however, the eggs are retained until they hatch in specialized portions of the female reproductive tract, and the offspring emerge as juveniles. Many of the Nematoda and all the Acanthocephala are endoparasitic forms with especially well-developed reproductive systems.

It will be recalled that one of the distinguishing characteristics of the true coelom is its consistent relationship to the reproductive system; this relationship can be demonstrated or inferred in all eucoelomate animals. In many of the more primitive annelids, for example, there are no permanent gonads or reproductive ducts. The peritoneal lining of the coelomic cavities is essentially a germinal epithelium, in which gametes are periodically produced and released into the coelom; the gametes reach the exterior by rupture of the body wall or by passage through the nephridial tubules. Sometimes special gonoducts have been developed to conduct gametes to the outside. At this primitive level copulation does not occur; male and female gametes are simply shed into the surrounding medium for external fertilization and development. The more highly evolved oligochaete annelids have permanent gonads and elaborate accessory chambers and ducts, which are clearly localizations and specializations of primitive coelomic structures and functions. The oligochaetes are almost entirely limited to fresh-water and terrestrial habitats, and the reproductive specializations, including copulation and the production of cocoons in which fertilization and development occur, may be interpreted as adaptations to environmental conditions.

Among mollusks and arthropods, in which the coelom is not well developed in the adult animal, the cavities within the gonads may be interpreted as coelomic spaces, lined by germinal epithelium, in which the gametes are produced. The reproductive ducts are gonoducts, retaining their primitive connections with the coelomic cavities. Among bivalve mollusks reproductive mechanisms are simple; fertilization often occurs within a part of the mantle cavity of the female, and early developmental stages may be passed within the "brood pouches" in the gills. In gastropods and cephalopods reproductive systems are much more complex. Here some kind of copulation is the rule; fertilization is internal, and the female reproductive system possesses elaborate glandular portions which secrete shells and egg cases about the zygotes. Although many snails are hermaphroditic, cephalopods are typically dioecious. Among Arthropoda reproductive mechanisms vary from relatively simple to highly complex; but even among the simple forms there is usually some kind of copulatory behavior, in which spermatozoa are transferred into a seminal receptacle of the female. In many crustaceans, such as the crayfish, this is an externally opening, sac-like pocket having no direct connection with the female reproductive system, and ova are fertilized externally as they pass the opening of the receptacle. In terrestrial forms, however, as in insects, the seminal receptacle is a diverticulum of the common oviduct, and fertilization is internal. Most insects deposit shelled eggs, well protected against damage or desiccation. In some of the highly evolved Diptera, the zygotes hatch within the body of the female, who then deposits active, first-stage larvae on or near sources of food. In other specialized dipterans, even the larval stages are passed within the reproductive system of the mother, and the offspring appear as fully mature larvae, ready to pupate. In at least one group of insects with parasitic larvae, early larval development is marked by polyembryonic reproduction reminiscent of that noted in larval trematodes.

Among Echinodermata, reproductive systems are comparatively simple. The gonads are sac-like or branching, tubular structures, and the reproductive ducts lead directly from the gonads to the exterior. In the adult there is no clear relationship between the gonads and the coelom, but in embryonic stages the genital rudiment develops in connection with other derivatives of the coelom. Reproduction in echinoderms never involves copulation or internal fertilization, but there are many instances in which embryonic development occurs within superficial brood pouches on the body of the female.

There are two special phenomena of reproduction that are of surprisingly general occurrence among invertebrates, although their distribution has no demonstrable relationship to phylogenetic position or affinities. These two phenomena are **hermaphroditism**, or **monoeciousness**, and **parthenogenesis**. In monoecious animals each individual of the species develops complete and functional reproductive systems of both male and female sexes. It is exceptional, however, for fertilization to involve spermatozoa and ova from the same individual. Most commonly, there appear to be special safeguards, either morphological, functional, or chronological, which prevent self-fertilization. In the earthworm, for example, the structural relationships are such that it is practically impossible for self-fertilization to occur. In some planarians it has been demonstrated that spermatozoa do not become active in the presence of ova from the same individual; and in many other monoecious animals the testes and ovaries do not become functional at the same time. Granting that such close inbreeding as self-fertilization would probably be detrimental, we are still faced with the problem of understanding why animals should be bisexual and yet be prevented from producing offspring in isolation, a process to which monoeciousness would seem primarily adapted. One provisional answer suggests itself. Usually a population consists of males and females in approximately equal numbers. This means that only half the random encounters between two individuals can be reproductively fruitful, since a given male will be as likely to encounter another male as to meet a female. If every individual is both male and female, however, then every encounter is doubly effective; insemination is mutual, and the eggs of both individuals can be fertilized as a result of a single meeting. It is perhaps significant that monoeciousness appears to occur most commonly among animals which are slow-moving and relatively inactive, or which inhabit environments that do not facilitate or permit frequent encounters between different individuals. Consider, as examples, the planarian, the snail, and the earthworm, and the helminth inhabiting the intestine of a vertebrate. Interpreted from this point of view, monoeciousness as it has developed among animals clearly confers certain selective advantages and is of definite survival value to a species.

Parthenogenesis is the process by which offspring develop from eggs that have not been fertilized. It should be understood that although parthenogenesis does not involve fusion of nuclear material from two individuals, it is not interpreted as asexual reproduction; it requires the production of a differentiated gamete from which the new individual arises. Parthenogenesis occurs in several diverse groups of invertebrates, notably among rotifers, nematodes, crustaceans, and insects. In many rotifers males are completely unknown, and reproduction is entirely a matter of the development of young females from unfertilized eggs produced by mature females. In other rotifers, and in some Cladocera among crustaceans, environmental changes in some way induce the periodic production of males, and syngamy then occurs. The resulting zygotes are usually covered with thick shells and are capable of withstanding unfavorable environmental conditions during their long period of incubation. Reference has been made to the interesting reproductive habits of the honeybee, in which the queen receives at one copulation all the spermatozoa she will use during her life to fertilize her eggs. The spermatozoa are stored in a seminal receptacle, and by opening or closing the duct leading from this chamber the queen is capable of what has been termed "facultative parthenogenesis." Most of her eggs are fertilized and so develop into diploid females, either workers or young queens. By withholding spermatozoa, however, the queen can deposit unfertilized eggs which develop into the haploid males called drones. Other insects, such as aphids, also have parthenogenetic reproductive mechanisms.

The diversity of structure and of functional adaptations in the reproductive systems of invertebrates has been sufficiently illustrated by the foregoing review. Obviously, there is little general similarity throughout the invertebrate groups, beyond the presence of ovaries, testes, and their respective ducts, although within a given phylum certain fundamental plans can be recognized. Further complications of the reproductive systems are related to the reproductive habits and modes of development in the many types of invertebrates, and adaptations to special environmental conditions can often be inferred. When these systems are compared from the standpoint of the functions of their parts, it is clear that similar functions have been assumed in many instances by structures that are not homologous. This is an indication that many different kinds of reproductive systems have arisen independently in the evolution of invertebrates. We may then conclude that in their evolution various kinds of animals have solved their common problems of reproduction in ways that are functionally comparable, although effected by different structures.

Summary

In this survey of the invertebrate groups we have considered the vital functions common to all, as well as the structural features which the functions involve and upon which they depend. The facts presented justify the general conclusion that whereas all organisms have been confronted with a relatively limited number of common problems of survival, in terms of vital functions, there is an almost unlimited number of solutions to the problems in terms of structural adaptations. In many groups of animals the structures developed for certain functions are homologous; in other groups structures of diverse embryonic origins have become adapted to serve common functions and are thus analogous but not homologous. It is also apparent that there are no discontinuities between vertebrates and invertebrates in functional considerations. There are, however, so many more types of invertebrates than of vertebrates that the range of structural adaptations possible among invertebrates is infinitely more varied than among vertebrates. Perhaps we should again emphasize the fact that the distinction between vertebrates and invertebrates is chiefly one of convenience and of itself implies no formal taxonomic differences.

With this chapter we conclude our discussions of major invertebrate phyla and turn to the phylum Chordata, which includes all the vertebrates as well as a few minor groups of invertebrates. One additional phylum, the Hemichordata, consists only of invertebrates, and this group is to be considered along with the chordates, to which it is obviously closely related.

CHAPTER 18

CHAPTER 18

THE PHYLA HEMICHORDATA AND CHORDATA

The phyla **Hemichordata** and **Chordata** consist of bilateral, triploblastic animals, usually with a well-developed coelom which primitively arises, as in echinoderms, by evagination from the embryonic gut. These animals commonly show evidences of metamerism, at least in some of their structures. The Chordata are further characterized by three fundamental features: (1) a dorsal, tubular central nervous system; (2) gill slits, or pharyngeal clefts, at least during a part of the life cycle; and (3) an extensive primary endoskeletal structure, the rod-like **notochord,** from which the name of the phylum is derived. Members of the phylum Hemichordata possess characteristics which are comparable with all of these, but which are present in a relatively rudimentary condition. The hemichords have pharyngeal clefts, sometimes well developed; the central nervous system has a dorsal component, although this is not the principal part of the system; and an endoskeletal structure resembling the chordate notochord is present but very limited in extent. This "half-chord" is responsible for the name Hemichordata. On the basis of these structural resemblances, the hemichords are often regarded as the most primitive members of the phylum Chordata. We shall consider them rather as the non-chordate phylum whose characteristics most closely approach those of true chordates. The hemichords, like the most primitive chordates,

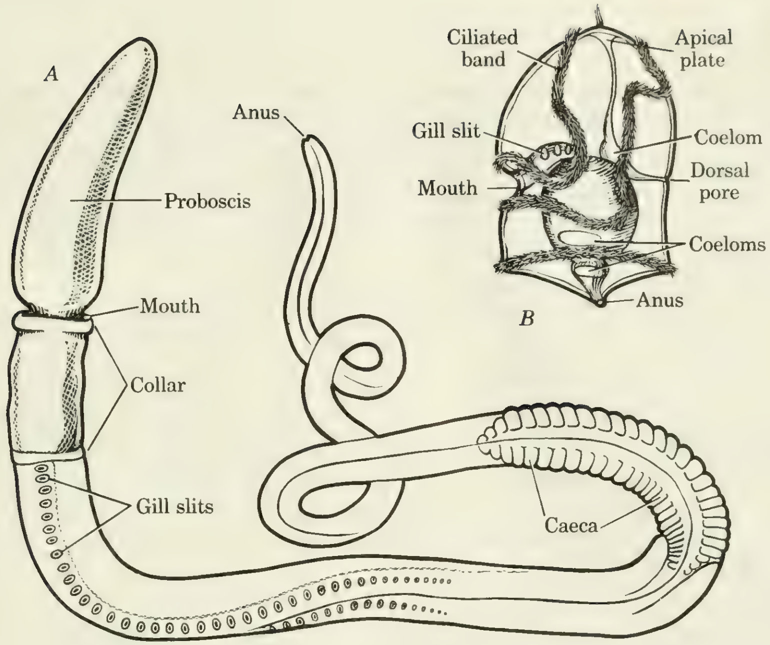


Fig. 18.1. Phylum Hemichordata. *A*, general features of a typical balanoglossid, *Saccoglossus kowalewskii*. *B*, general features of the tornaria larva, a free-swimming developmental stage in the life cycles of many balanoglossids.

are invertebrates; but their affinities with the phylum Chordata are so evident that we have reserved them for discussion with the chordates.

The Hemichordata constitute a minor group of invertebrates, exclusively marine, which are either sedentary, burrowing, worm-like forms or highly modified, sometimes colonial animals attached to the substrate or floating in the sea. In contrast, the Chordata are highly diversified, and they are in fact the most widely distributed group of animals, with the possible exception of the arthropods. They are found in the ocean at all depths, and on land from rain forest to desert habitats, and from the tropics to the polar regions, where representatives of the warm-blooded birds and mammals occur. Chordates range in size from minute forms to whales, which are the largest of existing animals. In diversity of habitat and structure, only the arthropods, again, rival the chordates. The distribution of arthropods on land is limited, however, by their inability to remain active at low temperatures; and even large arthropods, such as some crustaceans, are pygmies in comparison with the largest chordates.

The phylum Chordata comprises two large subdivisions; the division **Acraniata** and the division **Craniata** or **Vertebrata.** The Acraniata are those chordates without skulls and without vertebral columns, in which the notochord is the only skeleton. In some of these forms the notochord may persist only through the larval stages. The Craniata include the chordates with skulls and with vertebrae. In these the notochord always appears in early development, but it is subsequently more or less replaced by vertebrae, which form around it during the differentiation of the familiar cartilaginous or bony endoskeleton. The subdivisions of the Acraniata and Craniata, with their general characteristics, are outlined on pages 541 and 542.

It now appears probable that the fossils known as Graptolites represent extinct members of the phylum Hemichordata. If this interpretation of the evidence is correct, the fossil record of the hemichords extends from the Cambrian period (see Fig. 20.1, p. 617). The first recognizable remains of chordates appear as fossils in the Ordovician period, but it must be assumed that earlier types of chordates, lacking skeletal parts that could be preserved as fossils, existed long before this time. From the Devonian onward, the fossil record of the Chordata is more comprehensive than that of any other phylum. The study of the evolutionary history of the phylum Chordata is in part the study of the remote ancestry of mankind, since man is a chordate.

In this chapter we shall discuss briefly the phylum Hemichordata and its probable relationship to the Chordata, proceeding to a consideration of the chordates themselves. In earlier chapters, principles of vertebrate structure and function have been discussed so extensively that we shall now consider in detail only the chordates that are not vertebrates. For the vertebrates, we present in this chapter a survey of the principal types and their evolutionary history. In considering this history, we shall be anticipating the subject matter of a later chapter which deals with evolution in general. However, in dealing with the various invertebrate phyla we have outlined their apparent phylogenetic development and evolutionary history, and the vertebrates will be similarly treated. When we speak of "ancestors" and "descendants," as indicated from the fossil record, it will be with the understanding that the evolutionary interpretation is to be accepted as the most reasonable explanation of the facts. The specific evidence for evolution in general, with further examples of the evolution of vertebrates, will follow in Chapter 20.

In view of the frequent references to geologic time and to the fossil record which it is necessary to make in the present chapter, it is important that Figure 18.8, page 554, as well as Figure 20.1, page 617, be studied carefully and kept in mind. It is also important that the characteristics of the two phyla and their subdivisions be noted, as shown in the following classification.

PHYLUM HEMICHORDATA

Class Graptolithina (extinct). Colonial organisms, consisting of chains of zooids produced by budding from a common stolon, often attached to a bladder-like float. Rapidly evolving forms; the fossil remains are interpreted as representing five orders. Became extinct during the Carboniferous period. *Diplograptus* and many others (Fig. 18.2).

Class Pterobranchia. Small, sessile, or free-floating hemichords with a crown of tentacles and a U-shaped gut; often producing colonies by budding. *Cephalodiscus*, *Rhabdopleura* (Fig. 18.2).

Class Balanoglossida. Worm-like hemichords, with body conspicuously divided into proboscis, collar, and trunk regions. *Saccoglossus*, *Balanoglossus*, and others (Fig. 18.1).

PHYLUM CHORDATA

DIVISION ACRANIATA. Without a skull, or cranium, and without vertebrae or appendages.

Subphylum Urochordata or **Tunicata.** Adults hardly recognizable as chordates. Larvae, known as "tadpoles," with a notochord in the tail, with gill slits, and with a dorsal, tubular central nervous system. During metamorphosis the notochord is lost, the gill slits are modified into a pharyngeal basket, and the nerve cord is reduced to a ganglionic mass. Tunicates, or sea squirts, and many others (Figs. 18.3, 18.5).

Subphylum Cephalochordata. With some resemblances to the tadpoles of tunicates, and also to fishes; with persistent notochord and gill slits, with a persistent dorsal, tubular nervous system, but without a skull or vertebrae. The amphioxus or lancelet, *Branchiostoma (= Amphioxus)*, and others (Fig. 18.6).

DIVISION CRANIATA. With a skull, or cranium, and usually with vertebrae and paired appendages.

Subphylum Vertebrata. Identical with Craniata: only subphylum in this division.

SUPERCLASS PISCES. With gills, and usually with appendages, commonly represented by two pairs of fins suited for locomotion in water. The various types of fishes.

Class Agnatha. Without true jaws and without limbs. Extinct forms, the ostracoderms, a large group of primitive fishes bearing large scales. Existing forms, the lampreys and hagfishes, without such scales (Fig. 18.9).

Class Placodermi. Armored fishes of specialized type, extinct, and not closely related to any existing forms.

Class Chondrichthyes. Shark-like fishes, with exposed gill slits. Extinct forms with bony skeletons, existing forms with cartilaginous skeletons. Sharks, rays, skates, etc. (Fig. 18.10).

Class Osteichthyes. With bony skeletons, and with gill slits covered externally by an operculum. Include the lobe-finned fishes (mostly extinct), the numerous existing ray-finned fishes, and the lungfishes. Common marine and fresh-water fishes (Figs. 18.11, 18.12).

SUPERCLASS TETRAPODA. With lungs, and usually with appendages which are commonly represented by two pairs of limbs suited for locomotion on land. The air-breathing vertebrates.

Class Amphibia. Semiterrestrial and aquatic forms; cold-blooded; skin usually soft and moist; respiratory exchange usually by gills in larva and by lungs and skin in adult. Typically with eggs laid and developing in water. Salamanders, frogs, toads, etc.

Class Reptilia. Terrestrial or secondarily aquatic forms, covered with scales or horny plates. Cold-blooded; lung-breathing; typically oviparous, some ovoviviparous. Turtles, lizards, snakes, alligators, etc.

Class Aves. Terrestrial forms, usually adapted for flight, covered with feathers. Warm-blooded, lung-breathing, oviparous. Birds.

Class Mammalia. Terrestrial or secondarily aquatic forms, at least partially covered with hair. Warm-blooded, lung-breathing, with mammary glands. Mostly viviparous. Mammals.

The Phylum Hemichordata

The Balanoglossida: ***Saccoglossus.*** Species of this genus, and of such other genera as *Balanoglossus*, *Glossobalanus*, etc., are marine, worm-like animals that usually live in shallow water and are found burrowing in muddy or sandy bottoms. Externally, three body regions are apparent: the **proboscis,** the **collar,** and the **trunk** (Fig. 18.1). The mouth is located ventrally, just beneath the proboscis and within the anterior border of the collar; the anus lies at the posterior tip of the trunk. The gill slits form a dorsolateral row of perforations on each side in the anterior region of the trunk, extending posteriorly for some distance. These perforations are passages from the cavity of the pharynx to the exterior. Near the middle of the trunk region, transverse ridges are produced by paired, glandular caeca which arise from the digestive tract. The **digestive system** includes a buccal region within the collar, a pharyngeal region marked by the gill slits, and an intestine which bears the caeca and leads to the anus. As the animal burrows through sand or mud, the proboscis is thrust forward, and the silt from which food is extracted enters the mouth and pharynx. Excess water passes outward through the dorsolateral gill slits, aerating the blood in vessels lining their walls. The ingested silt, concentrated in a ciliated groove in the ventral region of the pharynx, is conducted posteriorly through the intestine, where usable food materials are digested and absorbed.

Coelomic spaces are found within proboscis, collar, and trunk, being derived from three pairs of primary embryonic coelomic pouches. The circulatory system consists of a median dorsal and a median ventral longitudinal vessel, interconnected by small lateral branches in the pharyngeal region and posteriorly. A so-called "heart" lies in the proboscis, but the blood is probably propelled chiefly by peristaltic contractions of the longitudinal vessels. A **glomerulus,** which has been considered an excretory organ, is connected with blood vessels in the proboscis.

The **nervous system** is composed of two principal nerve trunks formed as ectodermal thickenings in the median dorsal and median ventral regions of the trunk. These cords appear to represent specialized areas of a generally distributed subepidermal nerve net, or plexus layer. The cords are connected by a ring-like epidermal thickening in the collar, and the dorsal trunk proceeds anteriorly through the collar before dipping downward to enter the proboscis. The resemblance of this nervous system to the central nervous system of the typical chordate is not outstanding, although the nature of the dorsal nerve trunk in the collar region is somewhat suggestive of the chordate nerve cord. A structure called the **stomochord** is present in the posterior part of the proboscis, arising as an anterior extension from the dorsal wall of the buccal cavity. This small supporting element is probably homologous with the chordate notochord, but it is limited in its extent and of a very primitive nature.

The sexes are separate in the balanoglossids; the gonads are sac-like structures arranged serially on each side in the region of the genital ridges. When mature, each gonad establishes an individual, externally opening genital pore. The small eggs are fertilized externally, and development proceeds in the sea water. A pelagic, ciliated larva, the **tornaria** (Fig. 18.1), occurs as a developmental stage in the life cycles of some species, but not in *Saccoglossus*. The tornaria is so similar to the dipleurula-type larva of echinoderms that it was originally described as the larva of some unidentified echinoderm. This similarity may be interpreted as indicating an evolutionary relationship between echinoderms and hemichords, a relationship which is suggested also on the basis of certain biochemical similarities.

The Pterobranchia: *Cephalodiscus* and *Rhabdopleura*. These are small marine forms with the typical hemichord body regions of proboscis, collar, and trunk (Fig. 18.2); the internal anatomy is comparable with that of the balanoglossids. In correlation with their generally sedentary mode of life, the gut is U-shaped, the anus opening near the mouth. The proboscis is modified into two or many arms, or tentacles, which in *Rhabdopleura* are retractable into the secreted test within which the animal lives. Reproduction is both sexual and asexual; in *Rhabdopleura* new individuals are produced by budding from a horizontal stolon growing along the substrate. Individuals thus formed constitute a colony of zooids comparable with those of colonial coelenterates. The fossil remains of the extinct graptolites, long considered as either coelenterates or ectoprocts, have in the light of recent studies been interpreted as showing many similarities to the sessile and enclosed pterobranchs.

Relationships of the Hemichordata. In the phyla Echinodermata, Chaetognatha (p. 365), Hemichordata, and Chordata, the embryonic origin of the coelom is by the enterocoelous method, as in no other animal groups except the anomalous Brachiopoda (pp. 361-365). This common embryological feature is considered to indicate that these four groups are related by a common ancestry. Evidence from serological studies (see page 635) shows that the proteins of chordates resemble those of echinoderms and hemichords more closely than those of any other invertebrate group. Further, biochemical studies on substances termed **phosphagens**, important in the functions of muscular tissues, also reveal significant similarities between these three groups. The tornaria larva is suggestive of an evolutionary relationship between echinoderms and hemichords, and the presence in hemichords of visceral clefts, the stomochord, and rudiments of a dorsal nerve cord suggests affinities with the chordates. On the whole, the evidence may logically be interpreted as supporting the concept of a common evolutionary line of enterocoelous, deuterostomous organisms, possibly resembling the dipleurula or tornaria,

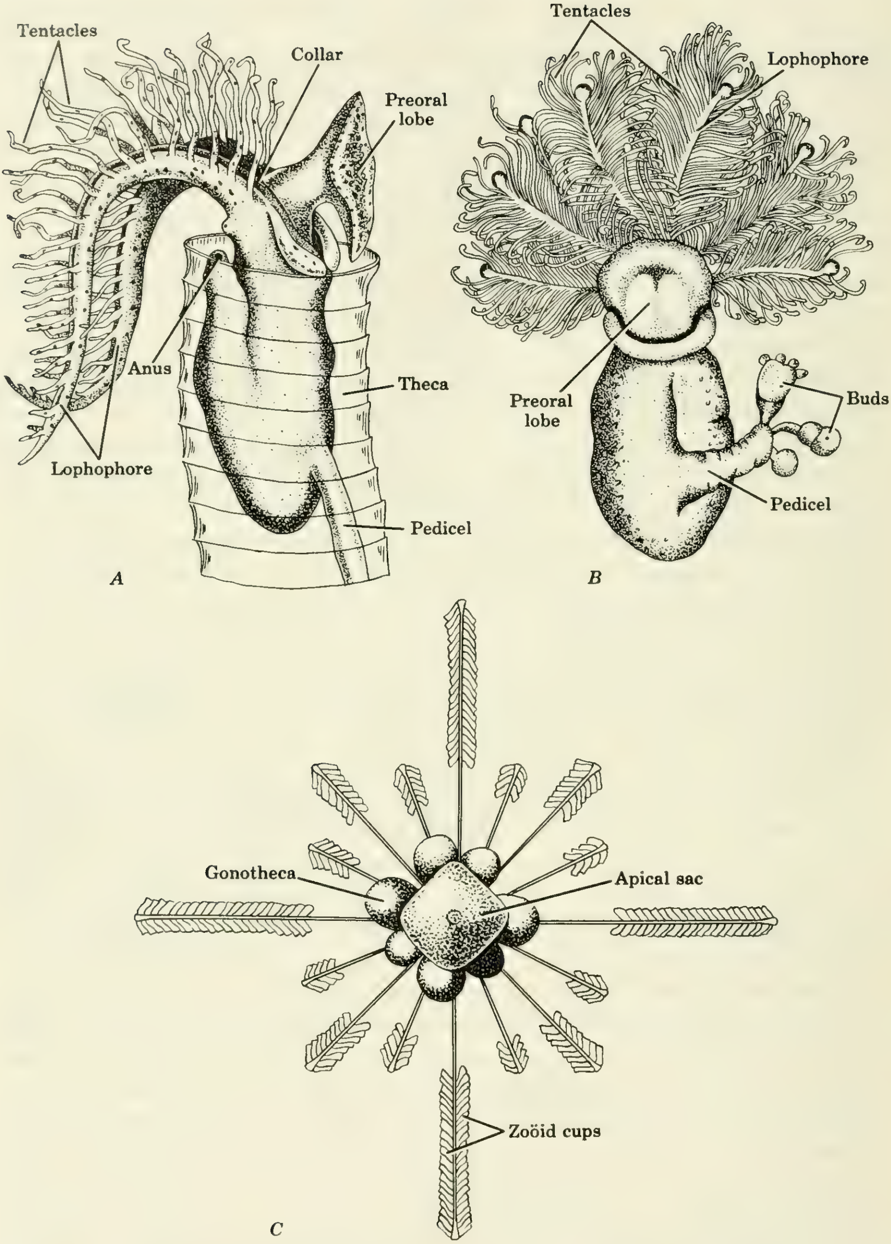

Tentacles
Collar
Preoral lobe
Anus
Theca
Lophophore
Pedicel
A
Tentacles
Lophophore
Preoral lobe
Buds
Pedicel
B
Gonotheca
Apical sac
Zoöid cups
C

Fig. 18.2. Phylum Hemichordata. *A*, general features of *Rhabdopleura; B*, *Cephalodiscus dodecalophus*, ventral view. *C*, reconstruction of what is interpreted as a floating community of colonies of the Ordovician graptolite *Diplograptus*, viewed from above. (*A* and *B*, redrawn from C. Dawydoff in P.-P. Grassé, Ed., *Traité de zoologie*, 1948, vol. 11, *A* after Delage and Hérouard, *B* after McIntosh; *C*, redrawn, after Ruedemann, from Y. Delage and E. Hérouard, *Traité de zoologie concrète*, 1901, vol. 2.)

from which by successive radiations the ancestors of the modern enterocoelous groups arose. The hemichords would seem to have evolved from this ancestral line after the divergence of the ancient echinoderms and chaetognaths but before the rise of the true chordates. These evolutionary changes must have antedated the beginning of our fossil record and undoubtedly involved small forms lacking hard parts.

The Phylum Chordata

THE ACRANIATA

The Urochordata. These organisms constitute one of the three subphyla into which the phylum Chordata is divided. They are invertebrates, in that they lack vertebrae, but their characteristics are unmistakably those of the chordates. The subphylum **Urochordata** includes the classes **Ascidiacea**, **Larvacea**, and **Thaliacea**, all of which are marine animals. Of these, the Ascidiacea, or sea squirts, are the best known; the Larvacea are an unusual type; and the Thaliacea are the most highly specialized.

The Ascidiacea. The important features of the ascidians are the specializations of the adult for an attached mode of life and the apparent evolution of the group from free-moving ancestors. On the basis of superficial and functional characteristics, ascidians were long classified as mollusks; it was not until their life cycles became known, in 1866, that the chordate nature of the early developmental stages was recognized. This establishment of relationship through the study of developmental stages is a celebrated event in the history of embryology.

The sea squirt, *Molgula manhattensis*, is one of the species of tunicates most abundant along the Atlantic coast of North America. *Molgula* is found attached to various submerged objects in shallow water, but it is most easily collected from the piling under wharves, where it is commonly associated with such other ascidians as *Styela* and *Ciona* (Fig. 18.3). An expanded *Molgula* appears as a globular mass attached at one end and having two tubular processes, the **siphons**, extending from the other. If an undisturbed specimen is observed, a gentle current of water may be seen entering the longer of these siphons and flowing outward from the shorter one. As in pelecypod mollusks (p. 372), the entire economy of the ascidian depends on these currents of water, which, again as in the mollusk, are maintained by internal ciliary activity. From the stream entering the incurrent siphon, the animal obtains its food by straining out minute organisms and particles of detritus; and the blood is aerated as the water passes through the modified gill slits. The feces and reproductive products are carried outward by the water as it flows through the atrium and the excurrent siphon.

In any typical ascidian the entire body is covered by a membrane, thick in *Molgula* and *Styela* but thinner in *Ciona*, termed the **test** or **tunic**. This

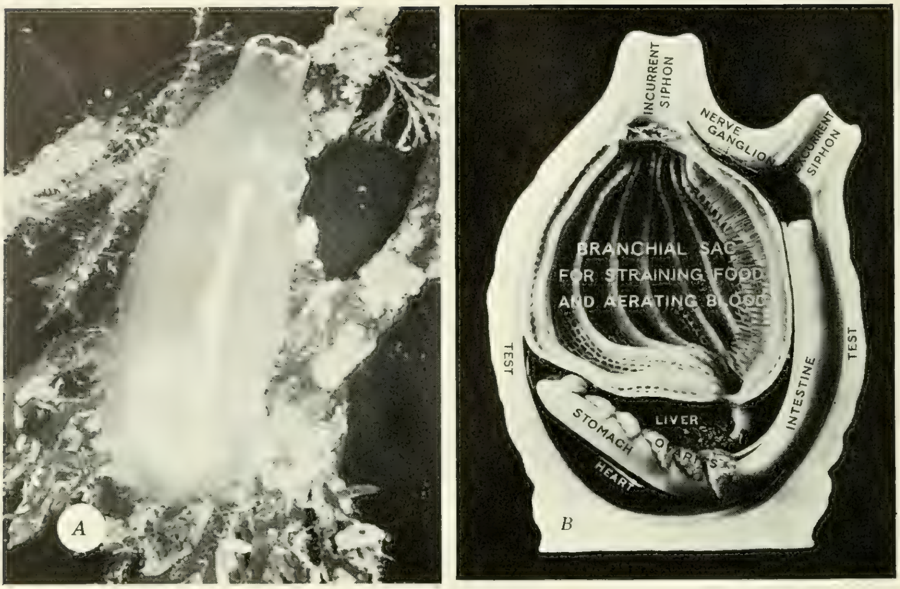


Fig. 18.3. Subphylum Urochordata: simple ascidians. *A*, *Ciona intestinalis*, general external appearance. *B*, internal anatomy of a sea squirt, *Molgula*. (*A*, photograph by George Lower; *B*, photograph of a model, courtesy American Museum of Natural History.)

is firmly attached to the body only in the region of the siphons and can be removed without disturbing the internal parts of the animal. The tunic functions as a tough, elastic shell, although it contains the cells by which it is secreted, as well as blood spaces through which nutrients reach these cells. The principal constituent of the test is an organic compound which has been named **tunicin**; this is very similar to cellulose, a compound common in plants but rarely produced by animal tissues. Removal of the test exposes the true outer surface of the body. Most of this surface is the so-called **mantle**, which encloses an extensive cavity, the **atrium**. The excurrent siphon is essentially a specialization of the mantle enclosing the median portion of the atrial cavity, from which lateral portions extend on each side beneath the mantle. Since the atrium is formed by the outgrowth of double flaps from the outer surface, it is lined by epidermal cells. The mantle consists of inner and outer epidermal layers, between which lie muscle fibers, connective tissue, and blood sinuses.

To understand the processes involved in feeding and in respiration, it is necessary to understand the structural relationships between the **digestive tract** and the atrium. The opening of the incurrent siphon may be called the mouth, and the cavity within this siphon, the oral cavity. A circlet of tentacles marks the beginning of the pharynx, or branchial sac, which is relatively large and specialized for food collection and aeration of the blood. The relationships between the siphons, pharynx, esophagus, stomach, intestine, and anus are apparent in Figure 18.3. A digestive gland is also present, connected with the stomach by a duct. Water passes into the mouth, enters the branchial sac, and passes through the many small openings in its wall into the atrial cavity on either side, and thence to the excurrent siphon, from which it is discharged. The openings in the branchial sac thus function in the manner of the less numerous openings called gill slits in other chordates. As in hemichords, food is obtained by straining the nutrient material from water received through the mouth and discharged through lateral openings in the pharynx. In the tunicate the food particles are caught in mucus as the water leaves the pharynx and are conveyed by ciliary currents along a specialized path to the esophagus; at the same time the oxygen dissolved in this water diffuses into the blood within the vessels of the pharynx.

The **circulatory system** consists of a tubular heart, lying along the outer curvature of the stomach, with tubules extending from one end directly to the pharynx and mantle, and from the other end to the stomach and nearby organs and thence to the pharynx. There are no true blood vessels, the blood circulating through extensive tubular cavities which lack an endothelial lining. The blood contains several kinds of free cells, some of which contain pigments which function in the transport of oxygen. A unique feature of the circulatory system is the periodic reversal of the heart beat; after the peristaltic waves of contraction have swept across the heart in one direction for a time, they cease, shortly to be resumed in the reverse direction. This brings about a corresponding reversal in the flow of the blood.

In the adult ascidian there is no cavity that can be called a coelom, unless the pericardium and the cavities within the excretory and reproductive organs can be so designated. Excretory functions are assumed for a mass of cells, without a duct, lying near the intestine; it has been shown to contain uric acid.

The **nervous system** consists of a single elongated ganglion, embedded in the mantle between the two siphons, and of sensory and motor nerves extending from each end of the ganglion to the siphons and other parts of the body. A glandular mass beneath the ganglion has been compared to the hypophysis of vertebrates.

Most tunicates are monoecious. The **reproductive system** includes an ovary and a testis, lying against the intestine, with ducts opening into the atrial cavity near the anus. In most of the solitary ascidians, such as *Molgula*, the gametes are discharged into the atrium, and fertilization occurs in this cavity or in the external water, where development takes place. The stages of cleavage and early differentiation are comparable with those of *Branchiostoma* (see Fig. 5.14). Embryonic development culminates in the appearance of a larva, the so-called **tadpole**, which possesses a dorsal, tubular nerve cord, a notochord, and gill slits (Fig. 18.4). Later, this larva becomes attached by suckers at its anterior end and undergoes a complicated metamorphosis, during which its more conspicuous chordate characteristics are lost or modified.

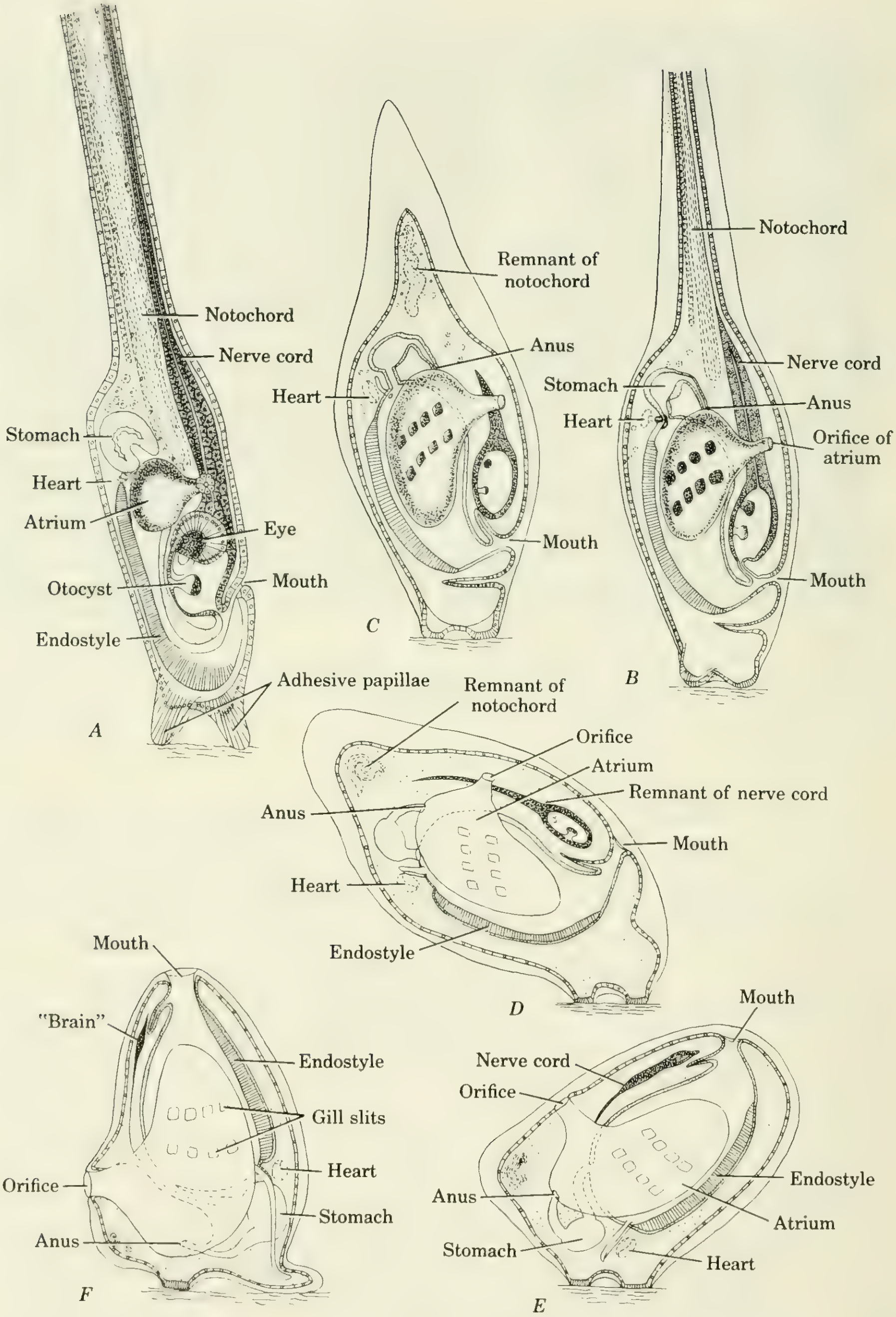
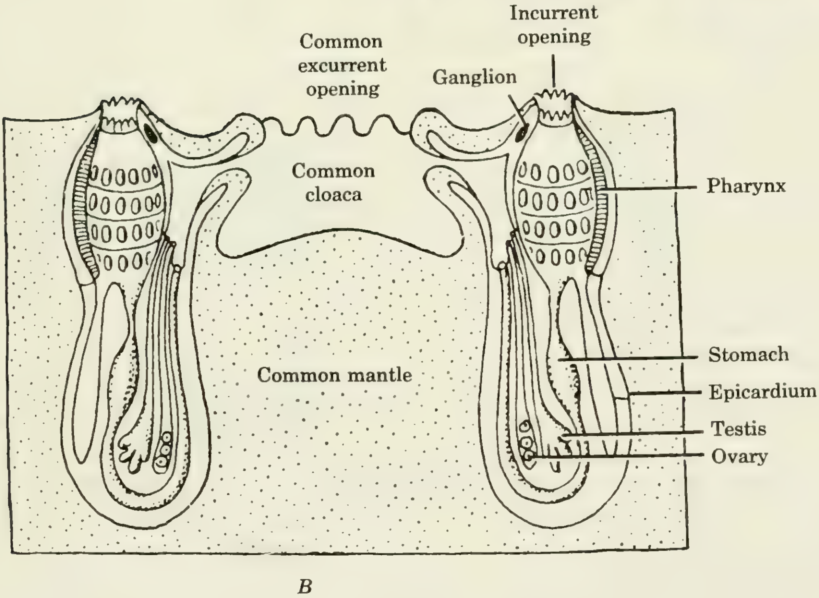

Notochord
Nerve cord
Stomach
Heart
Atrium
Eye
Otocyst
Mouth
Endostyle
Adhesive papillae
A
Remnant of notochord
Anus
Heart
Mouth
C
Notochord
Nerve cord
Stomach
Anus
Heart
Orifice of atrium
Mouth
B
Remnant of notochord
Orifice
Atrium
Remnant of nerve cord
Anus
Mouth
Heart
Endostyle
D
Mouth
"Brain"
Endostyle
Gill slits
Heart
Orifice
Stomach
Anus
F
Mouth
Nerve cord
Orifice
Endostyle
Anus
Atrium
Stomach
Heart
E

Fig. 18.4. Successive stages in the metamorphosis of an ascidian, from the attachment of the tadpole larva to the establishment of the adult form. Note particularly the degeneration of the tail and notochord, the extreme reduction of the nervous system, and the change in orientation of the mouth and digestive tract. (Redrawn, after various authors, from Y. Delage and E. Hérouard, *Traité de zoologie concrète*, 1898, vol. 8.)

Fig. 18.5. Compound ascidians. *A*, colonies of *Botryllus schlosseri;* the white stripes radiate from the common, central excurrent opening to the incurrent opening of each individual. *B*, diagrammatic vertical section through a colony, showing the relation of the individuals to the entire group. (*A*, photograph by George Lower; *B*, after O. Seeliger, from W. Stempell, 1926, *Zoologie im Grundriss.*)


Incurrent opening
Common excurrent opening
Ganglion
Common cloaca
Pharynx
Common mantle
Stomach
Epicardium
Testis
Ovary
B

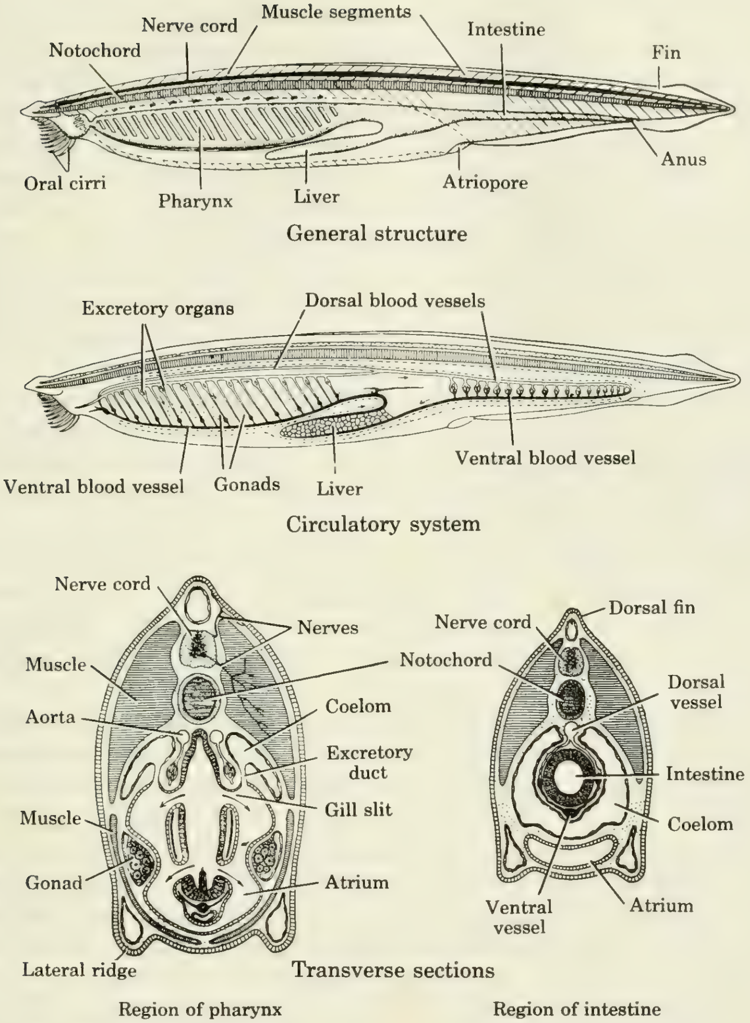
The notochord is resorbed along with the tail; the nerve cord coalesces to form the ganglion of the adult. The gill slits of the larva are subdivided and modified to form the many openings of the adult pharynx. This mode of development is most reasonably explained by the assumption that the modern, sessile tunicates have descended from primitive chordate ancestors that were not attached, but free-swimming, like the tadpole. It is on this basis, and because of the presence of such unequivocal chordate characteristics in the larva, that tunicates are classified within the phylum Chordata.

In contrast with the solitary ascidians, such as *Molgula*, *Styela*, and *Ciona*, the so-called compound ascidians are forms in which budding produces colonies of various kinds. In *Botryllus*, for example (Fig. 18.5), colonies consist of several individuals arranged radially about a common excurrent opening; each individual bears its own incurrent siphon. In *Perophora*, root-like extensions, or stolons, grow over a surface and give rise to additional individuals by budding. In most of the compound ascidians, the eggs are fertilized and development proceeds within the atrium, as far as the tadpole stage; the larvae are then discharged through the common excurrent atrial opening.

The Larvacea and Thaliacea. The Larvacea, which include only a few species of peculiar structure, resemble somewhat the larvae of the ascidians, rather than the adults. Whether they represent primitive, free-swimming forms or persistent larvae of forms which no longer undergo metamorphosis into sessile adults, is problematical. The **Thaliacea** include a wide range of forms, mostly unattached and with some feeble powers of locomotion but usually borne along by the currents of the ocean. They are clearly tunicates, although highly modified in comparison with the ascidians. Their anatomy and development indicate that they have evolved from ancestors which were attached like the ascidians. If this is true, their ancestry must have included primitive unattached types, then sessile forms, and finally secondarily free-moving organisms. Each of these phases has impressed its peculiar adaptive modifications on the animals as we know them. In some Thaliacea budding is extensively developed, and asexual generations alternate with sexual ones. Development in some species occurs within the parent, the embryo being attached by a placenta-like structure and nourished by diffusion of nutrients from the parent's blood. Familiar thaliacean genera are *Salpa* and *Doliolum*.

The Cephalochordata. The subphylum Cephalochordata contains only the class **Amphioxi**, a small group of marine animals long regarded as closely related to the Vertebrata. The indications are, however, that their affinities are with the tunicates, rather than with the vertebrates. It is suggested that the ancestors of the modern Amphioxi diverged from tunicate-like forms, giving up the attached mode of life to become free-swimming animals, and giving rise in the long course of evolution to the group which we term the cephalochordates.

The Amphioxi: Branchiostoma lanceolatum. Among the few genera that compose the class Amphioxi, the best-known species is *Branchiostoma* (= *Amphioxus*) *lanceolatum*, which occurs in European waters. The common name for this species is "lancelet," but the former generic name "Amphioxus" has come to be the usual designation. The animals are found in shallow water, buried in the bottom with the anterior end exposed, at rest on the bottom, or swimming freely. The body of the amphioxus (Fig. 18.6) is elongated and laterally compressed. A median dorsal fin, extending the length of the body, and a shorter ventral fin are specialized posteriorly to form a more conspicuous tail fin. Anterior to the ventral fin, two keel-like ridges extend along the ventrolateral margins, marking the positions of the


Nerve cord
Muscle segments
Intestine
Notochord
Fin
Anus
Oral cirri
Pharynx
Liver
Atriopore
Excretory organs
Dorsal blood vessels
Ventral blood vessel
Ventral blood vessel
Gonads
Liver
Nerve cord
Nerves
Muscle
Notochord
Aorta
Coelom
Excretory duct
Gill slit
Muscle
Gonad
Atrium
Lateral ridge
Nerve cord
Dorsal fin
Dorsal vessel
Intestine
Coelom
Ventral vessel
Atrium

General structure

Circulatory system

Transverse sections

Region of pharynx

Region of intestine

Fig. 18.6. Subphylum Cephalochordata: general structural features of *Branchiostoma*, the amphioxus or lancelet.

gonads. The mouth is located anteriorly within a hood-like structure, the edge of which forms a fringe of delicate processes called cirri. The anus is located on the left side, near the base of the tail fin. Another opening, the atriopore, lies just anterior to the ventral fin; it serves as the excurrent opening for water that has passed through the mouth and gill slits. The metameric arrangement of the musculature is conspicuous and may be seen through the thin epidermal covering of the body.

The **digestive tract** consists of a **pharynx**, or branchial sac, perforated by a series of paired **gill slits**, and an **intestine** leading posteriorly to the anus.

A sac-like **digestive gland,** called the liver, is attached by a duct to the anterior end of the intestine. The pharynx is surrounded laterally and ventrally by a cavity, the **atrium,** which is enclosed by flaps of the body wall fused along the midventral line. The atrium communicates with the exterior through the atriopore. In the normal activities of the animal, sea water is drawn into the mouth and pharynx through the space enclosed by the hood and cirri. From the pharynx the water passes through the gill slits into the atrium and outward through the atriopore. Microscopic food particles are strained from the water in the pharynx and passed to the intestine, as in tunicates. The action of ciliated cells lining the gill slits and other parts is principally responsible for maintaining the flow of water that brings in food materials and serves for gaseous exchange.

The **circulatory system** includes a **ventral blood vessel,** extending the length of the digestive tract, and a **dorsal vessel,** which is divided into right and left branches in the region of the pharynx. The dorsal and ventral vessels are interconnected, anteriorly by vessels in the walls of the pharynx and posteriorly by a network of vessels in the digestive tract and body wall. There is no heart, the circulation of the blood being brought about by peristaltic contractions of the longitudinal vessels. The course of the blood, anteriorly in the ventral vessel, upward in the vessels of the gill slits, and posteriorly in the dorsal vessel, resembles the course of circulation in vertebrate embryos and in fishes.

There is a conspicuous **coelom** in the region of the intestine, but anteriorly the coelom is reduced in the region of the pharynx. Numerous **excretory organs,** in the form of modified nephridia, open into the atrium; they occur in bilateral pairs and are segmentally arranged. It is a peculiar fact that solenocytic protonephridia also occur in the amphioxus. As seen in the intestinal region, the lateral parts of the body are largely occupied by the somatic musculature; anteriorly, the muscles fill only the dorsolateral quadrants. The **notochord** lies dorsal to the digestive tract, surrounded by the musculature; it is thus in a position completely comparable with that of the notochord in vertebrate embryos. The connective-tissue sheath surrounding the notochord extends dorsally as a sheath for the **central nervous system,** which is an axial, tubular cord resembling the spinal cord of a vertebrate. The cavity of this tube is slightly expanded at the anterior end, where there are a supposed olfactory organ and a median pigment spot. There is no anterior differentiation of the nerve cord that can be fairly called a brain, although two pairs of nerves extending anteriorly have been termed cranial nerves. Posterior to these, a large number of bilaterally paired nerves pass from the nerve cord in a metameric arrangement corresponding with that of the muscle segments. The cord contains photoreceptors in the form of pigmented, cup-like bodies.

The **reproductive organs** consist of paired gonads, segmentally disposed and lying in the lateral walls of the atrium, into which they project. The sexes are separate, and the gametes are discharged into the atrium by rupture of the walls of the gonads. The development of the amphioxus has been described in Chapter 5 (p. 147).

The chordate features of Amphioxi are readily apparent from the foregoing description. The dorsal, tubular central nervous system is formed from the dorsal ectoderm. The notochord is obviously comparable with that of the vertebrates, both in its structure and in its anatomical relationships to the nerve cord and the gut. The gill slits, the arrangement of the blood vessels, and the course of the blood flow, along with other resemblances, mark these animals as chordates, although they are much simpler in their organization than the most primitive fishes.

The Acraniata thus include two groups, Urochordata and Cephalochordata, which are evidently closely related, although they are widely divergent types. Evidence from comparative embryology and comparative anatomy indicates that these forms are also related to Vertebrata. The evolutionary changes through which the ancestral chordate stem produced these modern representatives must have occurred long before the Cambrian period, which explains the absence of a fossil record to document the steps or stages. Thus, in attempting to establish the relationships between Acraniata and Craniata, we must rely on embryological and anatomical evidence.

THE CRANIATA OR VERTEBRATA

A **skull**, or **cranium**, and **vertebrae** are the features that have given to these animals the names Craniata and Vertebrata, respectively. The skull encloses a **brain**, formed by the differentiation of the anterior end of the neural tube. Correlated with the development of the brain and its skeletal encasement is the fact that the notochord does not extend to the very anterior end of the body, as it does in the amphioxus. In all vertebrates the notochord appears during embryonic development. In many of the lower vertebrates it persists in the adult as a cord running through the center of each vertebra, but in

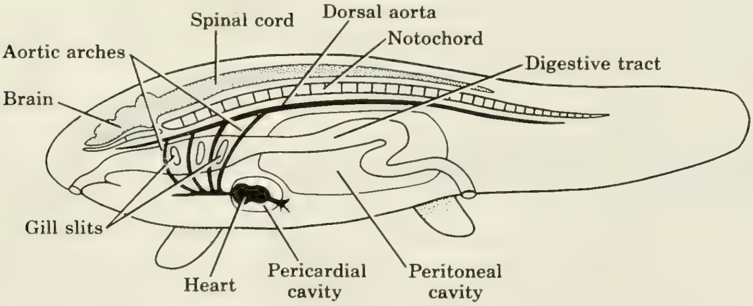


Fig. 18.7. Diagram of a generalized vertebrate, showing relationships of the chief internal structural features. Lungs, present in a great many vertebrates, and reproductive and excretory systems, present in all, are not indicated in this figure.

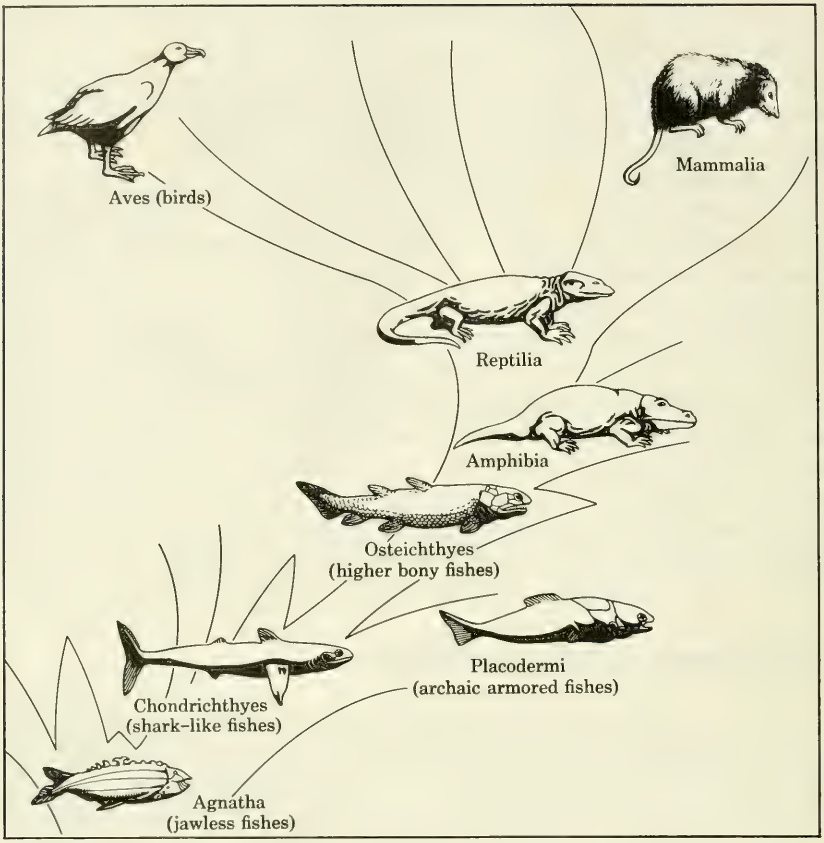

Aves (birds)
Mammalia
Reptilia
Amphibia
Osteichthyes
(higher bony fishes)
Placodermi
(archaic armored fishes)
Chondrichthyes
(shark-like fishes)
Agnatha
(jawless fishes)

Fig. 18.8. A simplified family tree of vertebrate groups. (From A. S. Romer, *Man and the Vertebrates*, copyright 1941 by University of Chicago Press, reprinted by permission.)

higher forms the primitive axial skeleton is replaced by the vertebrae. The great majority of vertebrates have paired **appendages**, either fins or limbs. The pharynx is of moderate size and bears **gill slits**, which are permanent in the lower forms but transitory in the vertebrates which develop lungs. The vascular system is closed, with a well-developed heart and blood containing red cells, or erythrocytes. Additional features of the vertebrates include paired eyes and ears, cranial and spinal nerves, a coelom, and a single pair of gonads. The relationships of some of these structures are represented in Figure 18.7, a diagram of a generalized vertebrate. Separation of the Vertebrata into gill-bearing forms with fins, the **Pisces**, and air-breathing forms with limbs, the **Tetrapoda**, reflects the apparent evolution of these animals from an aquatic to a terrestrial mode of life.

The Pisces or Fishes. As the first type of vertebrates (Fig. 18.8) known from the fossil record, the Pisces have had a long and diversified history.

There are reasons for believing that the earliest known fishes, the Ostracodermi (Fig. 18.9), lived in fresh water and perhaps originated there. The ocean was subsequently invaded by some of their descendants, which thus became the first marine fishes. The earliest complete skeletons of ostracoderms have been found in Silurian strata, although numerous bony scales from the Ordovician are regarded as fragments of similar animals. Along with primitive representatives of the Osteichthyes, the modern types first appeared in the Devonian as primitive sharks, representing the Chondrichthyes.

The Agnatha, or Jawless Fishes. The only living members of the class Agnatha, the lampreys and hagfishes (Fig. 18.9), are **round-mouthed and jawless**, with a **single nostril** on the dorsal side of the head, **without appendages**, with a **persistent notochord**, and with **rudimentary vertebrae**. The extinct ostracoderms are also classed as Agnatha; their fossil remains show that they were round-mouthed and jawless and that some, at least, possessed a single nostril. The hags and lampreys of the present time appear to be the lone

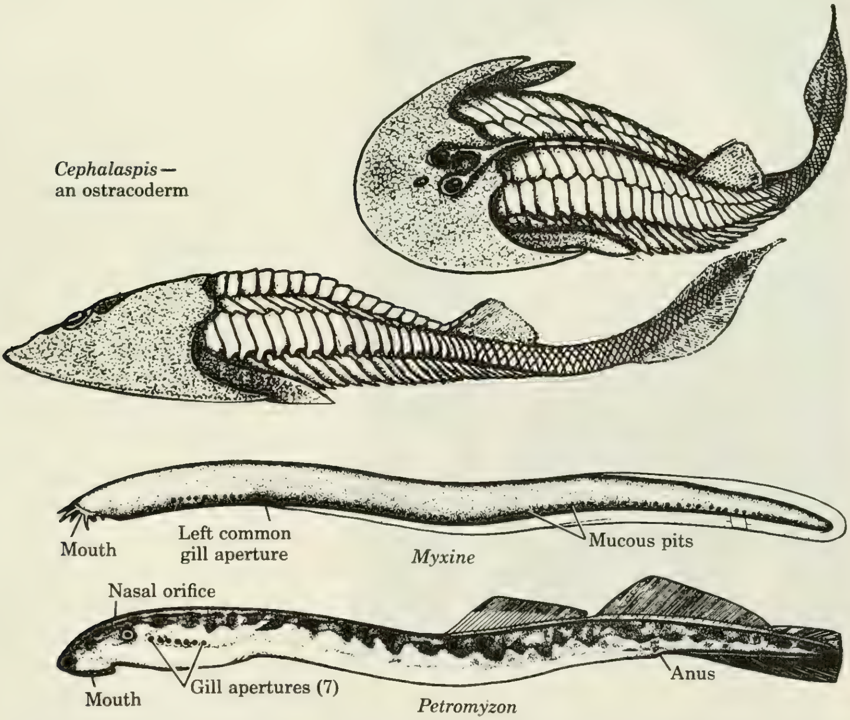


Fig. 18.9. Ancient and modern Agnatha, or jawless fishes. Fossil remains of the ostracoderm *Cephalaspis* are among the oldest known vertebrate fossils. *Myxine* and *Petromyzon* are characteristic genera of existing lampreys and hagfishes, lacking jaws and paired appendages. (From H. V. Neal and H. W. Rand, *Chordate Anatomy*, copyright 1939 by McGraw-Hill Book Co., Inc., reprinted by permission; *Myxine* and *Petromyzon* after B. Dean.)

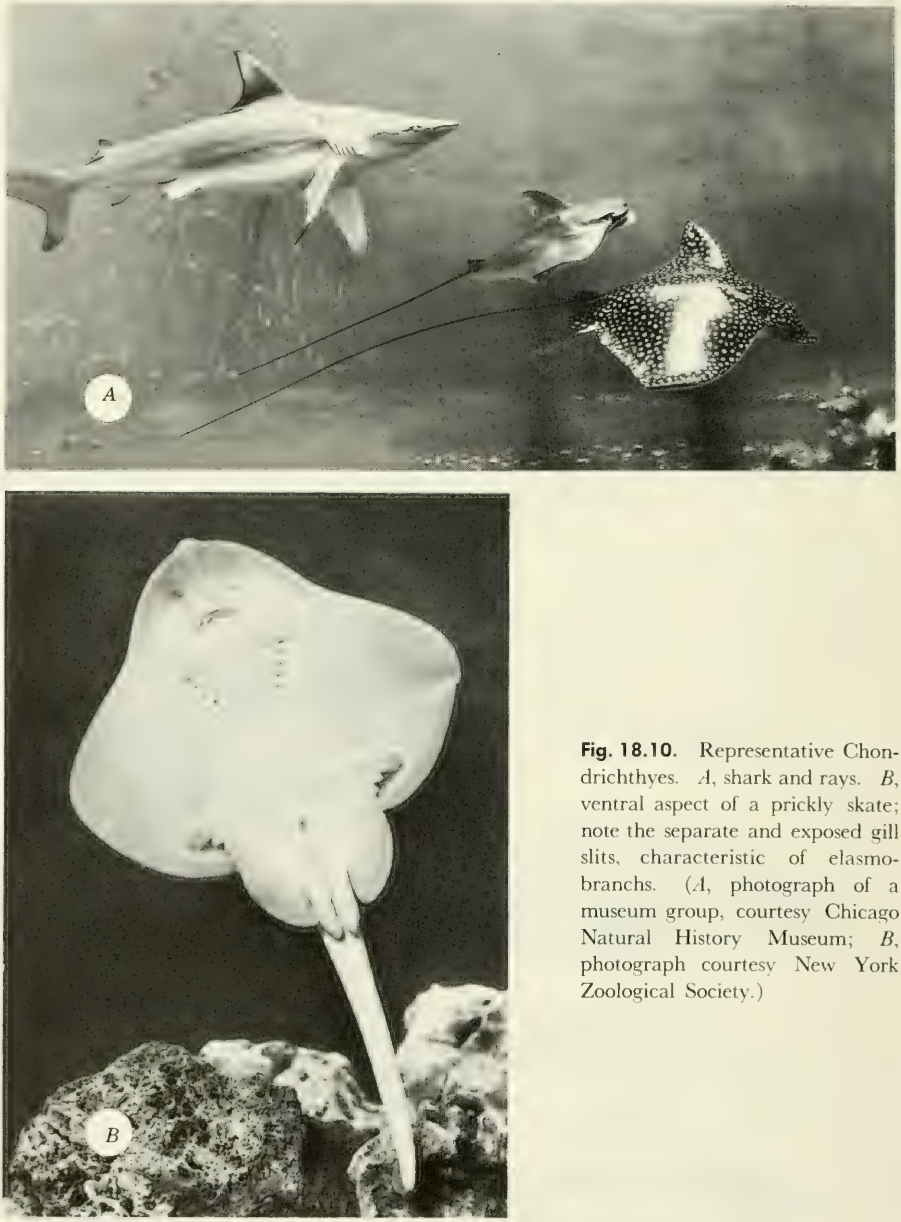


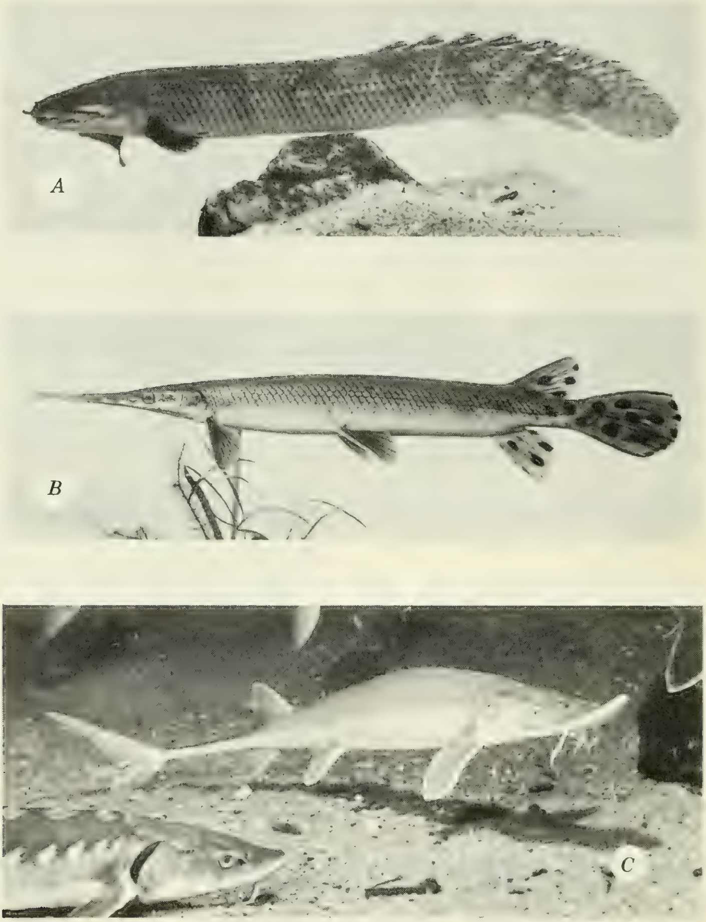
Fig. 18.10. Representative Chondrichthyes. *A*, shark and rays. *B*, ventral aspect of a prickly skate; note the separate and exposed gill slits, characteristic of elasmobranchs. (*A*, photograph of a museum group, courtesy Chicago Natural History Museum; *B*, photograph courtesy New York Zoological Society.)

survivors representing the earliest type of fishes, although they are a highly specialized and perhaps degenerate group. A lamprey feeds by attaching its sucker-like mouth to the surface of another fish and abrading the flesh with its inner mouth parts. The mouth is also used for holding to stones in swift water. The hags likewise feed upon other fishes, becoming attached and rasping their way into the flesh to such an extent that they can almost be regarded as internal parasites. Both lampreys and hags are represented by only a few genera, distributed in the ocean and in fresh water.

The Chondrichthyes. This class includes sharks, skates, and rays (Fig. 18.10). In contrast to the Osteichthyes, these fishes have a cartilaginous endoskeleton. This was long regarded as a very primitive feature in the evolution of vertebrates, but it now appears that the earliest known Chondrichthyes had bony skeletons. Thus, the existing forms must represent a line of descent in which the skeleton has degenerated from an earlier bony type to its present cartilaginous condition. Obvious specializations of the Chondrichthyes beyond those of the Agnatha include **biting jaws**, **teeth**, and **paired fins**. The jaws appear to have developed from certain skeletal bars of the gill region, and the teeth from scales similar to those in the skin of a modern shark. Sharks' teeth and remnants of the skeletal elements of the skin, well developed in many of the early forms, are much more abundant as fossils than are other remains of these animals. The fossils in some of the Devonian deposits, however, have enabled palaeontologists to make fairly complete restorations of types that were primitive, yet specialized in their own ways. The primitive sharks apparently originated in fresh water, from some ostracoderm stock, and subsequently migrated to the ocean. They then disappeared from fresh water. Ever since this invasion of the ocean, sharks of many kinds have been among the largest of the marine fishes. They are now familiar predators of the surface waters in the ocean, where they attack a wide range of prey. The skates and rays, with their specializations for life on the bottom of the ocean, represent divergent types. They commonly live in shallow waters, feeding upon mollusks, crustaceans, and other sluggish bottom-dwelling animals. The sting ray, with a venomous spine in its tail, and the torpedo ray, with a powerful electric organ, are highly specialized representatives of this group.

The Osteichthyes. In contrast to the existing Agnatha and Chondrichthyes, with cartilaginous skeletons, most members of the class Osteichthyes (Figs. 18.11, 18.12) have bony skeletons; however, the bones of this skeleton are not so firmly articulated as those of land vertebrates. As we have seen, bone did not originate with the Osteichthyes; it was present in the skeletons of early Agnatha and Chondrichthyes. The first representatives of the Osteichthyes appear as fossils in the middle Devonian, soon after the earliest sharks. These early Osteichthyes are separable into two groups, the **ray-finned** and the **lobe-finned fishes**. From the ray-finned group have descended the modern ray-finned fishes; from the early lobe fins have descended both the land vertebrates (Tetrapoda) and the existing lungfishes, called **Dipnoi**.

Surprising as it may seem, **lungs** appear to have been present in many, if not all, of these early fishes. Perhaps lungs arose as an adaptation favoring survival in stagnant pools which may have been formed recurrently in the watercourses, under the climatic conditions of the Devonian. After making a beginning of air breathing, one line of early fishes, the lobe-finned fishes,



probably gave rise to the Amphibia and so to the land vertebrates before it became extinct. Another line, the ray-finned fishes, was ancestral to the bony fishes of the present, in which the primitive lung was transformed into a hydrostatic organ, the swim bladder.

It is significant in this connection that the most primitive of existing ray-finned fishes, such as *Polypterus* (Fig. 18.11), the "bichir" of the Nile, retains the lung in its original function. Another and independent survival of the primitive lung appears in the three genera of lungfishes or Dipnoi, *Ceratodus* of Australia, *Protopterus* of South Africa, and *Lepidosiren* of South America. In these, the lung functions in respiration as an accessory to the gills, particularly in times of drought and stagnation of the water in which they live. In North America, the sturgeon, *Scaphyrhynchus*, the paddlefish, *Polyodon*, the gar pike, *Lepidosteus*, and the bowfin, *Amia*, are ray-finned fishes of a primitive type. The more specialized ray fins include

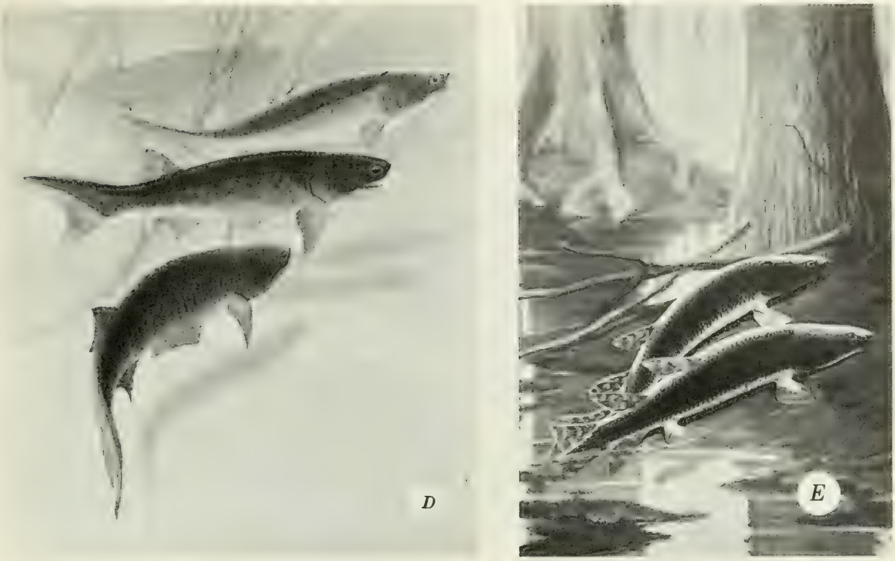


Fig. 18.11. Primitive fishes, living and extinct. *A*, *Polypterus*, the "bichir," one of the most primitive of existing ray-finned fishes. *B*, *Lepidosteus*, a gar pike, and *C*, *Scaphyrhynchus*, the shovel-nosed sturgeon; these are less ancient but comparatively primitive ray-finned types. *D*, restoration of *Cheirolepis*, one of the first of the ray-finned fishes, which flourished during the Devonian period. *E*, restoration of the lobe-finned fish *Eusthenopteron*, which also lived in Devonian times but which appears to have been closer to the line of fishes ancestral to later tetrapod types. (*A*, *B*, and *C*, photographs courtesy New York Zoological Society; *D* and *E*, from paintings by F. L. Jacques, courtesy American Museum of Natural History.)

all the most familiar fishes of fresh and salt water, such as trout, salmon, carp, bass, perch, catfish, cod, herring, mackerel, and many others. Although they are all modifications of the ray-finned type of fishes, the diversity of these forms is amazing. Almost every kind of shortening, lengthening, and flattening can be found in one species or another, along with such extreme modifications as those of the pipefish, toadfish, seahorse, flying fish, flounder, and the luminescent fishes of the depths of the ocean.

The Pisces, living and extinct, are thus the basic type among vertebrate animals. Appearing first in the fossil record, they include at the present time descendants of Devonian types, such as sharks, which are flourishing if not large groups, as well as groups living and extinct that suggest the beginnings of vertebrate life on land. Originating in fresh water, as the fossil record indicates, the Pisces have invaded the ocean and since that time have inhabited both fresh and salt water. The story of the ancient lung

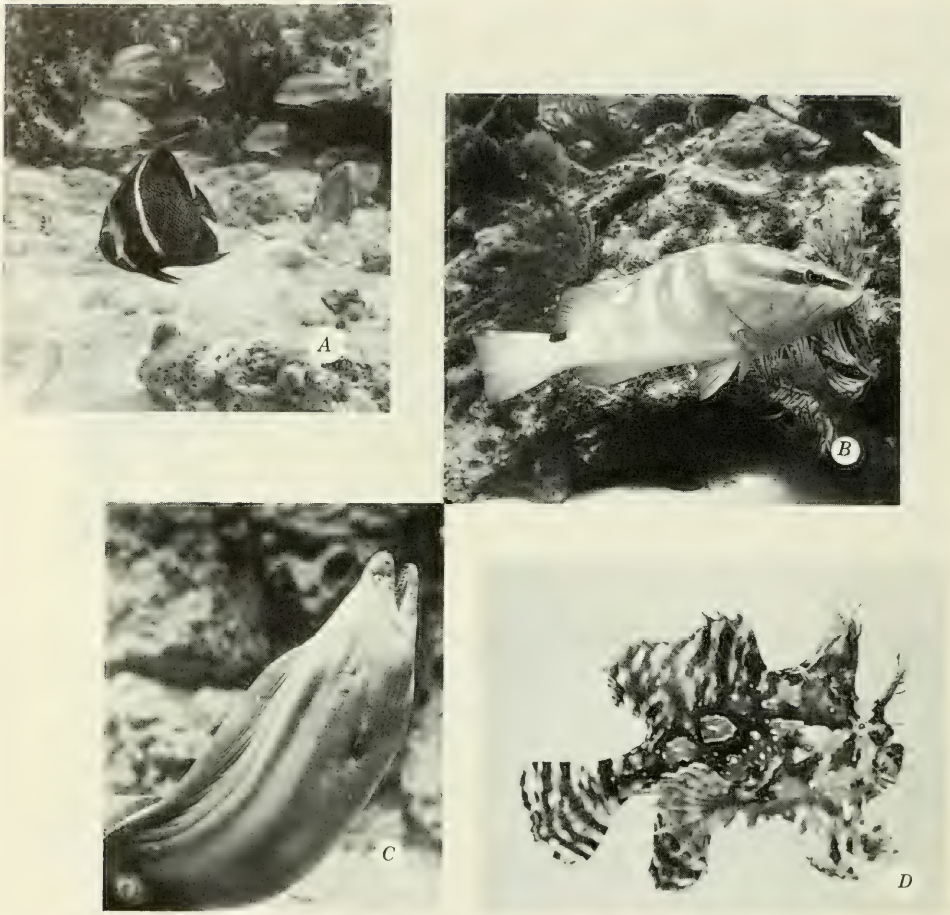


Fig. 18.12. Modern ray-finned fishes. *A*, an angel fish, *Pomacanthus*, of tropical marine waters. *B*, Nassau grouper, *Epinephelus*, in its natural reef habitat. *C*, green moray, *Gymnothorax*. *D*, the grotesque Sargassum fish, *Histrio*, found in floating beds of Sargassum weed which it strongly resembles. (*A* and *B*, underwater photographs by John F. Storr. Others, photographs courtesy New York Zoological Society.)

breathers, from which terrestrial vertebrates arose and whose lung breathing has survived in the two independent lines of lung-breathing fishes, is paralleled by other fishes coming out of the water in a variety of ways, in response to the struggle for existence along recent shorelines. At the other extreme are the fishes that have invaded the depths of the ocean and have been modified no less remarkably than those that invaded the land, whose descendants became the terrestrial vertebrates.

The Tetrapoda or Four-Footed Vertebrates. Within recent years, skeletal remains of very primitive amphibians have been found in the late

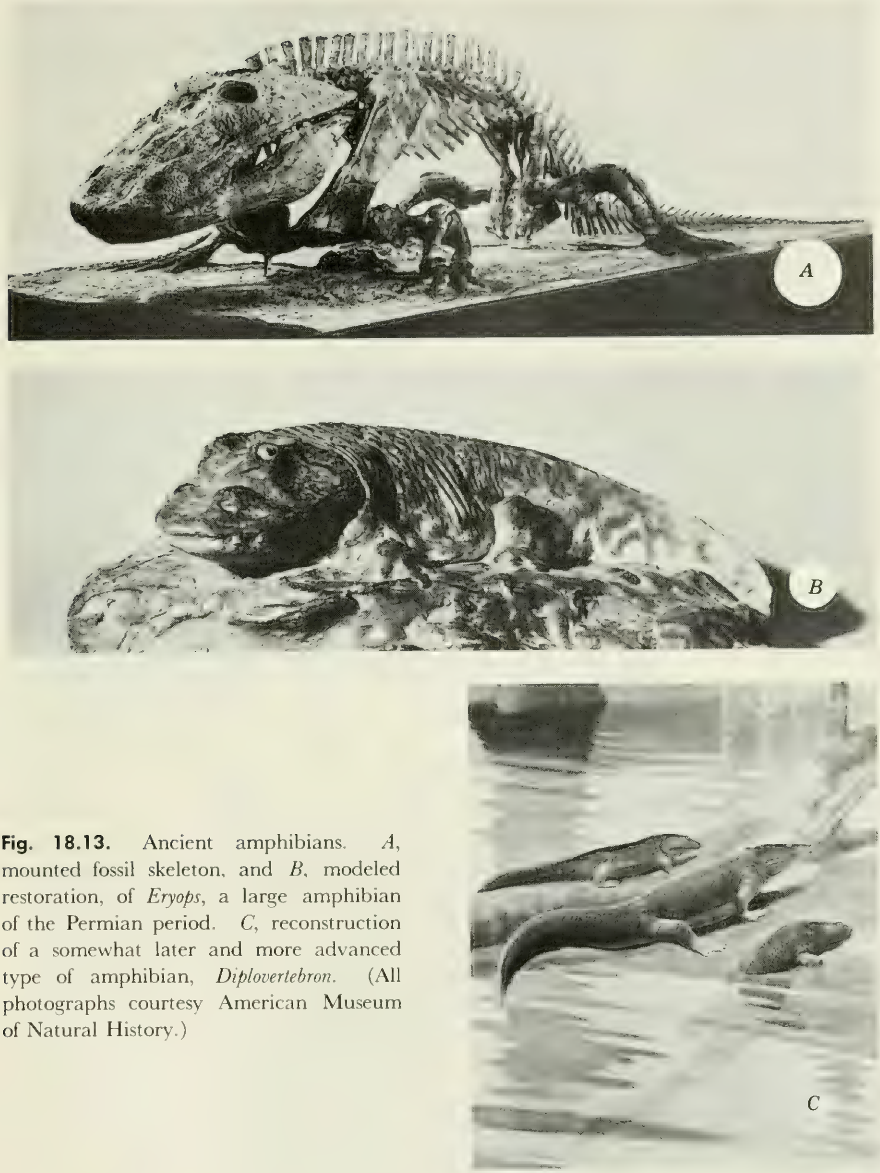


Fig. 18.13. Ancient amphibians. *A*, mounted fossil skeleton, and *B*, modeled restoration, of *Eryops*, a large amphibian of the Permian period. *C*, reconstruction of a somewhat later and more advanced type of amphibian, *Diplovertebron*. (All photographs courtesy American Museum of Natural History.)

Devonian of Greenland; these are the earliest traces of terrestrial vertebrates. This confirms the belief that the well-developed forms of the Carboniferous deposits (Fig. 18.13) were preceded by earlier amphibians in the Devonian or Silurian. The evolution of these early amphibians must have involved a long period of transition, during which fins became limbs and air breathing became an increasingly important mechanism of respiration. Clearly, the first terrestrial vertebrates were Amphibia, and they arose from lobe-finned fishes (Fig. 18.11). It will be recalled that these fishes were already provided with lungs; the bones of their fins are closely comparable with those of the limbs in amphibians. It is from these primitive four-footed land animals that the descent of all the later terrestrial vertebrates may be traced. If we put together what we know from the fossils and from the geological formations, it seems probable that the factors influential in the change of habitat from water to land, and in the evolution from four-finned to four-footed vertebrates, were such that early land animals were led to seek water rather than land. Droughts appear to have been frequent in the Devonian; it is thought that forms capable of moving across country "when the food failed and the last water dried" survived, whereas those that persisted as lobe fins gradually became extinct. Whatever may have been the course of events, the changes in structure and in habitat were effected. With the spread of these early terrestrial forms and the decline of the fishes came the Age of Amphibians, the first act of the evolutionary drama during which the four-footed vertebrates came to possess the land.

The Amphibia. Most amphibians of the present day remain half water dwellers and half land dwellers; they lead a "double life," as their name indicates. Although amphibians typically have well-developed lungs, these organs are supplemented by "skin breathing" in most species. The **tadpole** stage of amphibians is fish-like, not only in structure but also in habitat and activities. The earliest amphibians available as fairly complete skeletons resemble both the lobe-finned fishes and the reptiles. It appears that the early amphibians gave rise to certain specialized types which became extinct, to the ancestors of modern amphibians, and to the ancestors of reptiles. Among the primitive types were those called Stegocephalia, or "roof-headed," because of their heavily armored skulls (Fig. 18.13). Other forms were lean and active swimmers, as indicated by the characteristics of their skeletons. The conspicuous dermal plates, like those of fishes and reptiles, which were present in many early amphibians, have disappeared in modern forms. The limbs were used in locomotion, but they did not carry the weight of the body, which still trailed along the ground and probably aided in movement by sinuous undulations. The separation of oxygenated from unoxygenated blood in the circulatory system was presumably incomplete, as in the amphibians of today (p. 52). With the divergence of the reptilian line, the extinction of highly specialized types, and the differentiation of the surviving lines, the evolution of the modern forms was well on its way when the Age of Amphibians drew to a close. The flourishing of amphibians was probably correlated with the absence of other large land animals as competitors and with the swampy conditions that prevailed in Carboniferous times. Toward the end of the Permian, competition with the reptiles, a type better adapted for terrestrial life, and the advent of drier terrestrial conditions, were perhaps important factors in the decline of the amphibians. In any event, the Amphibia of today are small in size and few in number by comparison with those

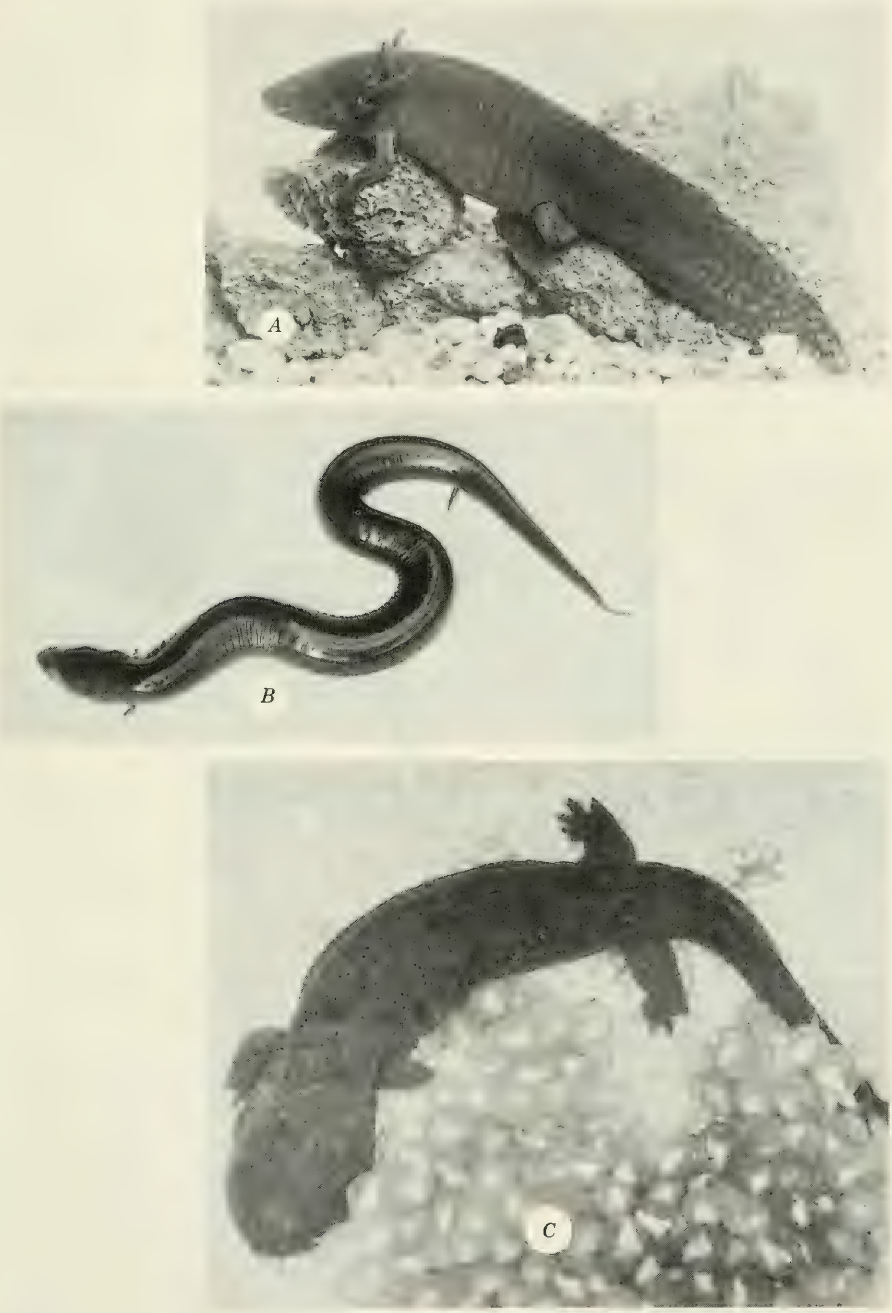


Fig. 18.14. Representative modern Caudata, or tailed amphibians. *A*, *Ambystoma tigrinum*, the axolotl, a permanently aquatic salamander with persistent external gills. *B*, the Congo snake, *Amphiuma*, with very small limbs. *C*, the hellbender, *Cryptobranchus*, here shown with a mass of developing embryos. (All photographs courtesy New York Zoological Society.)

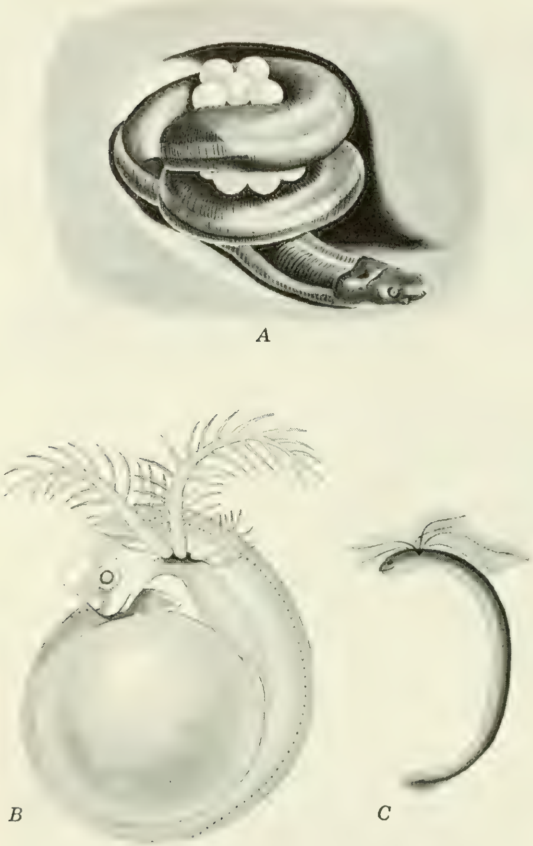


Fig. 18.15. *Ichthyophis*, a limbless amphibian or caecilian. *A*, adult in its burrow with a mass of eggs. *B*, young larva removed from eggshell; note the large external gills and the copious yolk supply. *C*, older larva after resorption of yolk but before loss of the external gills. (Redrawn from P. and F. Sarasin, 1887–1890, *Ergebnisse naturwissenschaftlicher Forschungen auf Ceylon*, vol. 2.)

of the past. They have survived like an entire group of "living fossils," insofar as they represent the fishes that emerged to the land but returned to water for their developmental stages.

Among existing amphibians the most generalized are the **Caudata**, or tailed forms, such as the salamander, *Ambystoma* (Fig. 18.14), and the mud puppy, *Necturus*. *Ambystoma* lives most of the year upon the land, returning to water for breeding in early spring. *Necturus* can live only in the water, since it depends on gills which are comparable with the external gills occurring temporarily in the development of other amphibians. An extreme type among the Caudata is the "Congo snake," *Amphiuma*, of the southeastern United States (Fig. 18.14). This animal may reach a length of 3 feet; its limbs are so reduced that the heavy-bodied animal is snake-like in appearance. Another large form is the "hellbender," *Cryptobranchus*, of the eastern United States (Fig. 18.14). The largest of existing amphibians, attaining a length of almost 6 feet, is the giant salamander of Japan, *Megalobatrachus*.

The order **Apoda,** limbless amphibians, is represented by a few small forms found only in the warmer parts of the world. Examples are *Ichthyophis*, of Ceylon (Fig. 18.15), and *Siphonops*, of South America (see Fig. 7.1, p. 215). These amphibians are burrowing animals about the size of large earthworms. Their developmental stages are passed in the burrow, within eggshells resistant to desiccation, but the larval stages possess external gills and other features characteristic of the aquatic stages of the Caudata and Salientia. The limbless state of the Apoda is a highly specialized characteristic, but in more important internal features they are among the most primitive of living amphibians.

The order **Salientia** contains the most familiar amphibians, the "leapers," comprising the many species of frogs and toads (Fig. 18.16). The line of descent for this modern type was apparently established at the close of the Age of Amphibians, but they were not clearly differentiated until the Age of Reptiles was well advanced. Existing species of Salientia are widely distributed, and on the whole they are the most highly specialized of the modern forms. Most species can live for long periods out of water if the atmosphere is sufficiently moist, and some, such as the toad, *Bufo americanus*, are more nearly land animals than any other amphibians. Even toads, however, are dependent on a moist atmosphere, and they return to ponds and streams during their brief breeding season in the spring. The frogs are even more dependent on water and a moist atmosphere, because of their greater use of the damp skin in gas exchange.

The general distribution of most amphibians is therefore conditioned by the requirements of each species, particularly in connection with their "skin breathing" and with their aquatic breeding habits. None of these forms is truly a terrestrial animal like the reptile, which very often lives and breeds in hot, dry places.

The Reptilia. Reptiles are "cold-blooded," air-breathing vertebrates, typically covered by horny **epidermal scales** and often with an underlying armor of bony **dermal plates.** There are also characteristic but less conspicuous features of internal anatomy. In contrast with amphibians, which are typically dependent on a moist atmosphere and water for reproductive and developmental stages, reptiles are completely adapted for terrestrial life. They live upon the land, even under desert conditions, and breed and undergo embryonic development without dependence on water. Perfection of lungs and air breathing, development of integuments and egg membranes which resist desiccation, and certain modifications of embryonic development are features that make possible this complete adaptation for terrestrial life. Arising from amphibian ancestors, reptiles became the dominant land animals of the Age of Reptiles and eventually gave rise to birds and to mammals. The reptilian manner of development, as compared with those of amphibians and mammals, represents a vital step in vertebrate evolution. Most reptiles are **oviparous.** The reptilian embryo, like the amphibian, develops in a fluid medium, but its medium is the amniotic fluid (see p. 162); the protective egg membrane prevents drying. There is a much larger amount of yolk than in the eggs of amphibians, and the time of hatching in reptiles is delayed until the young have reached the stage of juveniles able to care for themselves. Some reptiles have been modified from this state and have become **ovoviviparous;** that is, zygotes are retained within the body of the female, and development proceeds in a specialized portion of the female reproductive tract. Comparison of mammalian development with that of reptiles makes it evident that the viviparous development of most mammals has evolved from oviparity like that of reptiles. Indeed, the members of one group of primitive mammals, including the duckbill and the spiny anteater, still lay eggs.

The earliest known reptiles are from the Carboniferous (Fig. 18.17). These primitive types, or "stem reptiles," from which the later members of the class seem to have arisen, are so like amphibians that they might be classified in either group. The short limbs extend laterally rather than downward from the body, and it is evident that in life the body still rested upon the ground as it does in amphibians. The diversification of reptiles from the stem forms began in the Permian; as the Amphibia declined, the Reptilia became the predominant land vertebrates during the Mesozoic. Among the lines that flourished, only to become extinct with the rise of the Mammalia in later times, were the **dinosaurs** (see Figs. 18.19, 18.25, 18.27), the most diversified group of terrestrial vertebrates that has ever lived. Related forms were the **ichthyosaurs** and **mosasaurs** which invaded the sea (Fig. 18.18); the **pterosaurs,** flying reptiles distinct from the line giving rise to the birds (Fig. 18.19); reptiles ancestral to the birds themselves (see Fig. 18.25); and reptiles ancestral to mammals (see Fig. 18.29). The existing reptiles are remnants of a mighty race, of which at one time the dinosaurs ruled the land, the ichthyosaurs the water, and pterosaurs the air. We can only guess at the factors involved in the decline of such a group. Reptiles flourished as animals that were obviously better suited to terrestrial life than amphibians,

and the land was at that time occupied by no other large animals. Perhaps inability to maintain a constant body temperature, and brains smaller than the lumbar enlargements of their spinal cords, were important in the decline of reptiles when the Age of Mammals began.

Among living reptiles the members of the order **Chelonia,** or turtles and tortoises, represent the most primitive type, although superficially they may seem most specialized (Fig. 18.20). The box tortoise, *Terrapene*, and the painted tortoise, *Chrysemys*, are familiar examples. *Chrysemys*, and more particularly the soft-shelled tortoise, *Amyda*, illustrate forms that have shifted from land to water. This change of habitat has occurred in many types of reptiles since their original adaptation for terrestrial life. The Chelonia are fundamentally air-breathing land animals, but some of them, both fresh-water and marine species, have come to live partly in the water. These forms still breathe air and still come to land for their egg-laying. The extinct plesiosaurs and mosasaurs were reptiles that evidently lived in a similar fashion and presumably laid their eggs on land, as the dinosaurs seem to have done. There is evidence, however, that the ancient marine ichthyosaurs were ovoviviparous and hence more completely adapted to aquatic life. Among existing chelonians, an extreme development of size is seen in the giant tortoise of the Galápagos Islands and in the large marine turtles. These are dwarfs, however, in comparison with some of the ancient turtles.

A lone survivor of another primitive type, the order **Rhynchocephalia,** is the genus *Sphenodon* (Fig. 18.21L), now found only in New Zealand. *Sphenodon*, the "tuatera," is of great interest to the comparative anatomist because it represents a very generalized and primitive type of reptile. It is more closely related to the lizards and snakes than to other familiar forms.

The lizards (**Lacertilia**) and the snakes (**Ophidia**) are so closely related that they are placed together in the order **Squamata.** The fossil record indicates

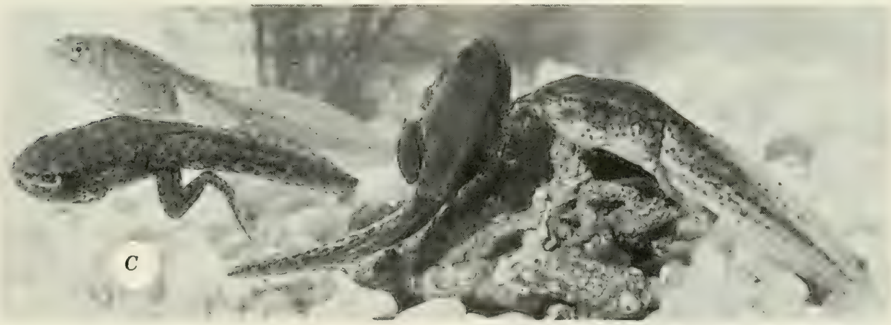


Fig. 18.16. Representative Salientia, or leaping amphibians. *A*, a toad, *Bufo americanus*. *B*, a spring peeper, *Hyla crucifer*, calling, its vocal sac distended with air. *C*, tadpoles of the green frog, *Rana clamitans*, some ready for metamorphosis to adulthood. (*A*, courtesy General Biological Supply House, Inc.; others, courtesy New York Zoological Society.)

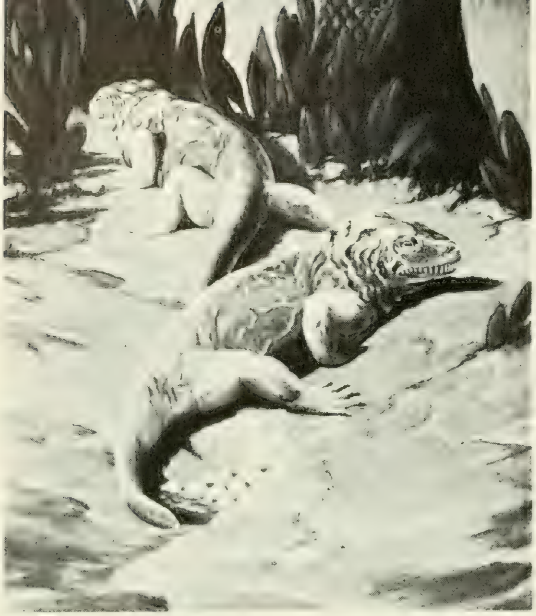


Fig. 18.17. Reconstruction of *Seymouria*, a problematic vertebrate from the Permian of Texas. *Seymouria* had many reptilian characteristics but retained also a number of amphibian features. It is usually assigned to a primitive group of reptiles, and in this reconstruction the artist has assumed that it produced typical reptilian eggs, like those known for other early reptiles. (Photograph courtesy American Museum of Natural History.)

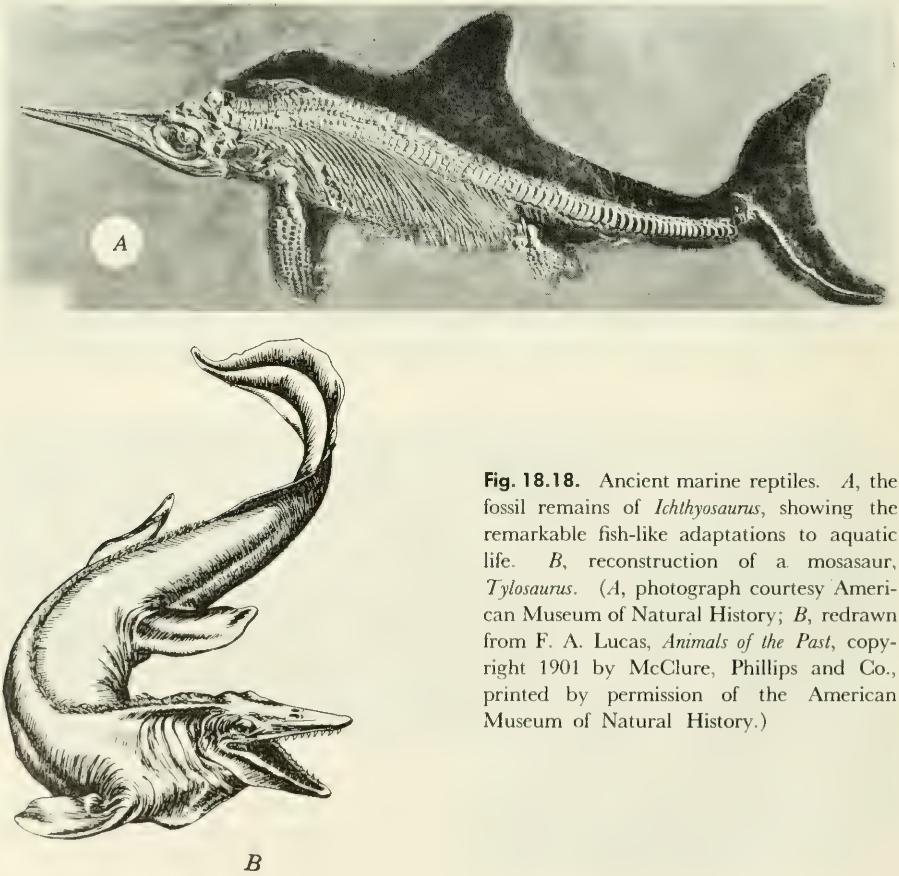


Fig. 18.18. Ancient marine reptiles. *A*, the fossil remains of *Ichthyosaurus*, showing the remarkable fish-like adaptations to aquatic life. *B*, reconstruction of a mosasaur, *Tylosaurus*. (*A*, photograph courtesy American Museum of Natural History; *B*, redrawn from F. A. Lucas, *Animals of the Past*, copyright 1901 by McClure, Phillips and Co., printed by permission of the American Museum of Natural History.)

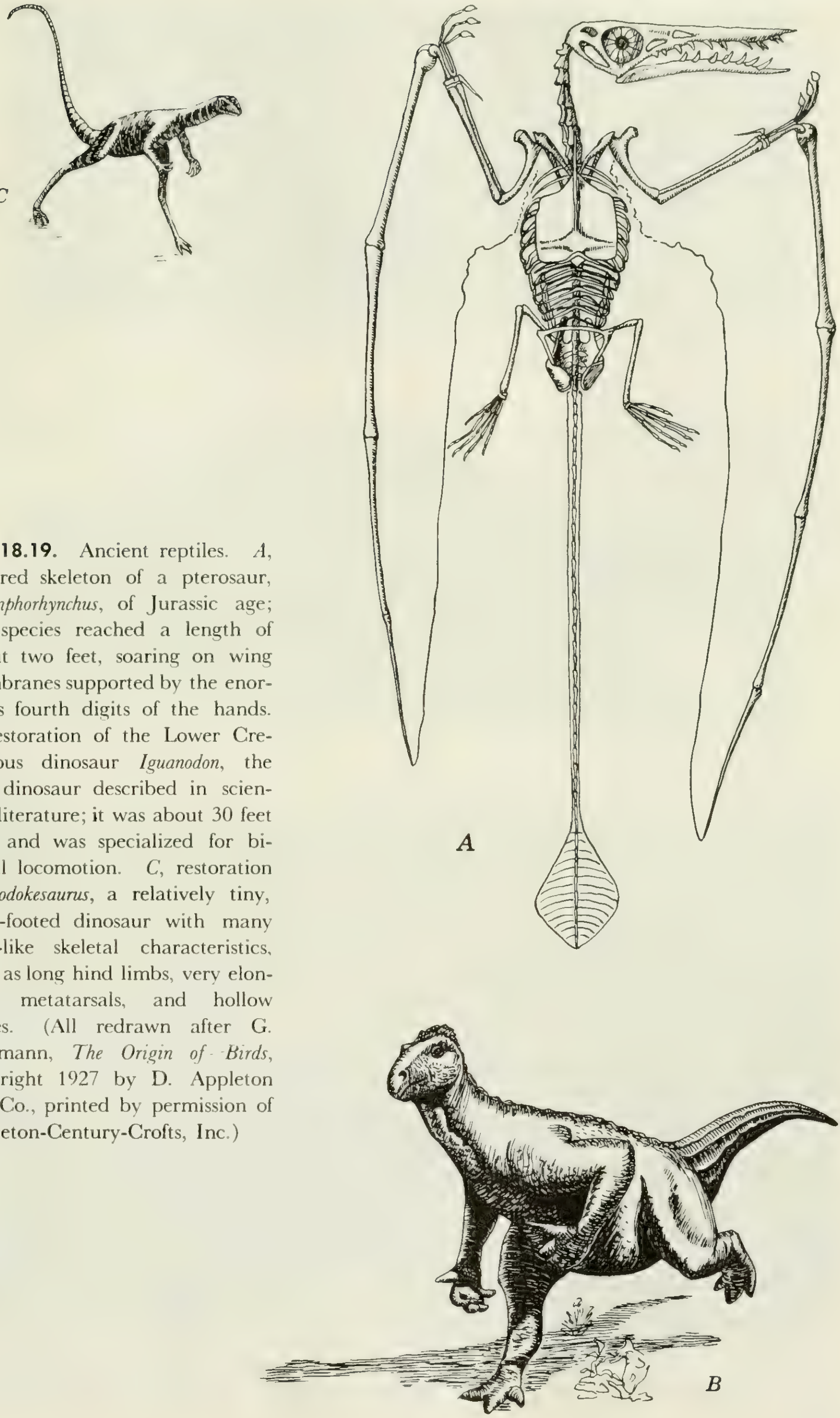


Fig. 18.19. Ancient reptiles. *A*, restored skeleton of a pterosaur, *Rhamphorhynchus*, of Jurassic age; this species reached a length of about two feet, soaring on wing membranes supported by the enormous fourth digits of the hands. *B*, restoration of the Lower Cretaceous dinosaur *Iguanodon*, the first dinosaur described in scientific literature; it was about 30 feet long and was specialized for bipedal locomotion. *C*, restoration of *Podokesaurus*, a relatively tiny, light-footed dinosaur with many bird-like skeletal characteristics, such as long hind limbs, very elongate metatarsals, and hollow bones. (All redrawn after G. Heilmann, *The Origin of Birds*, copyright 1927 by D. Appleton and Co., printed by permission of Appleton-Century-Crofts, Inc.)

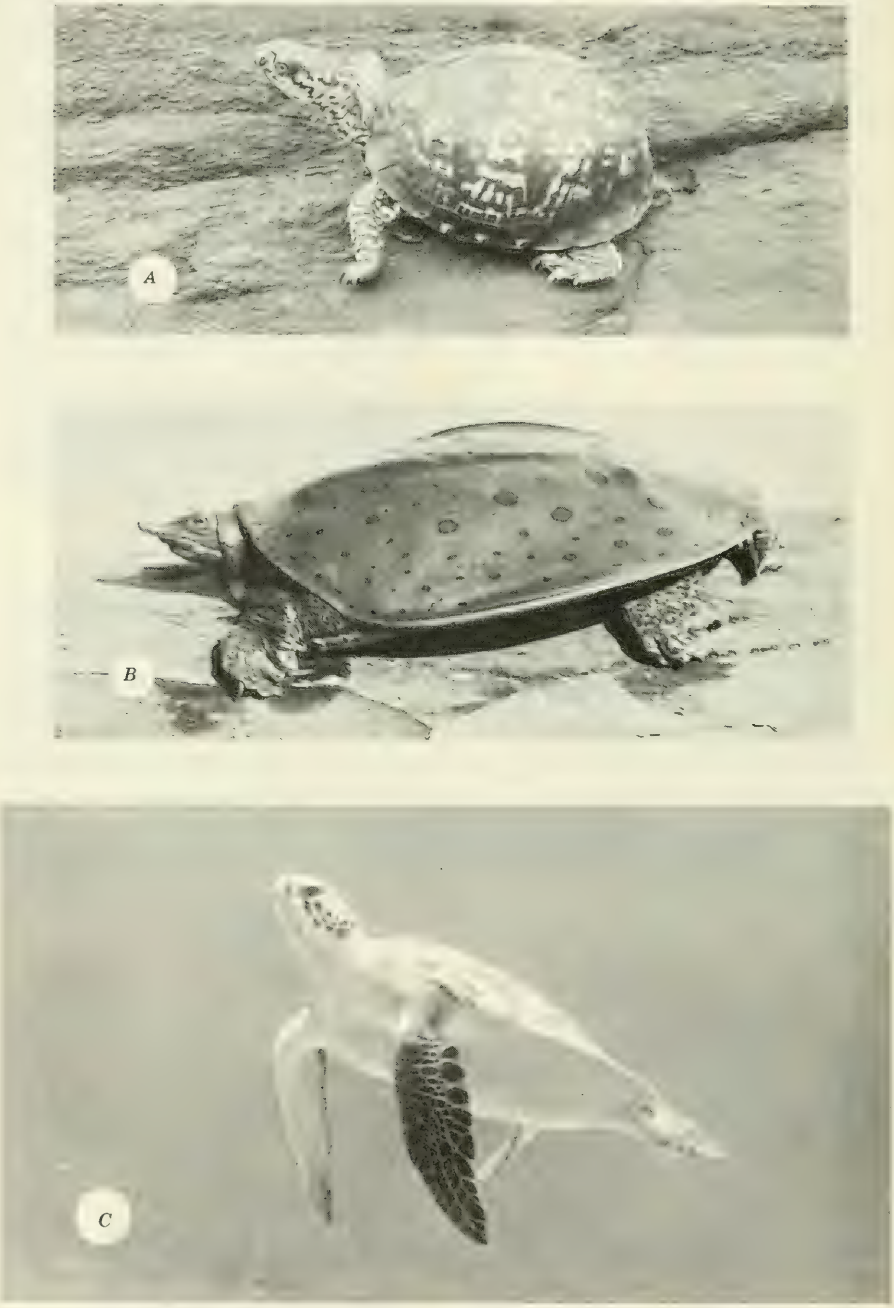


Fig. 18.20. Modern chelonians, terrestrial and aquatic. *A*, common box tortoise, *Terrapene carolina*. *B*, a soft-shelled tortoise, *Amyda spinifera*. *C*, a marine turtle, *Caretta*. (*A* and *B*, photographs courtesy New York Zoological Society; *C*, underwater photograph by John F. Storr.)

that snakes are a comparatively recent offshoot from four-footed ancestors within this order. There are also a few limbless lizards now living that resemble snakes but have had an independent and more recent origin. The various lizards in the warmer parts of the United States are familiar examples of the Lacertilia. The giant monitor lizard, *Varanus komodoensis*, of Java, one of the largest of existing reptiles, reaches a length of 10 feet and a weight of 250 pounds (Fig. 18.22). The African chameleon is a bizarre, slow-moving lizard noted for its ability to adjust its color to match that of the background. It feeds chiefly on insects, which it captures by means of a prehensile tongue that can be protruded with great rapidity to a length of several inches.

The snakes are a very specialized though recent reptilian type. In most genera the limbs have disappeared, but in a few, such as the pythons, minute vestiges are visible externally. Modifications of the ribs and vertebrae adapt the body for lateral coiling, and for locomotion by pushing and bracing the epidermal scales against the substrate. The jaws and related bones are modified in such a manner that the mouth can be stretched enormously in feeding. The viscera are also greatly modified in correlation with the elongation of the body. The **fangs** of poisonous snakes, such as the rattlesnake, are modified teeth associated with glands by which the **venom** is secreted (Fig. 18.23). In contrast with this means of offense and defense, the non-venomous boas and pythons, which attain great size, overpower their prey by crushing it in their coils. The great majority of our common snakes are quite harmless, and such species as the bull snake render great service to man by their destruction of rodents. Most species of lizards and snakes are **oviparous** in the typical reptilian manner (Fig. 18.23); a few species, such as the water snake, *Natrix*, are **ovoviviparous**.

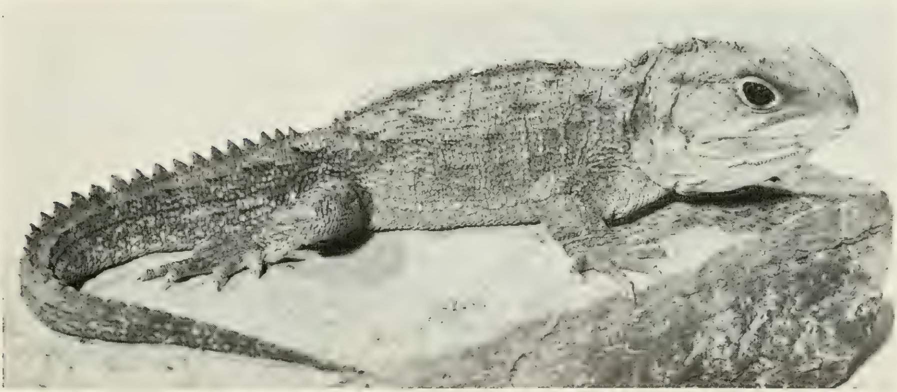


Fig. 18.21. *Sphenodon punctatus*, the only existing species representing the reptilian order Rhynchocephalia. (Photograph courtesy New York Zoological Society.)

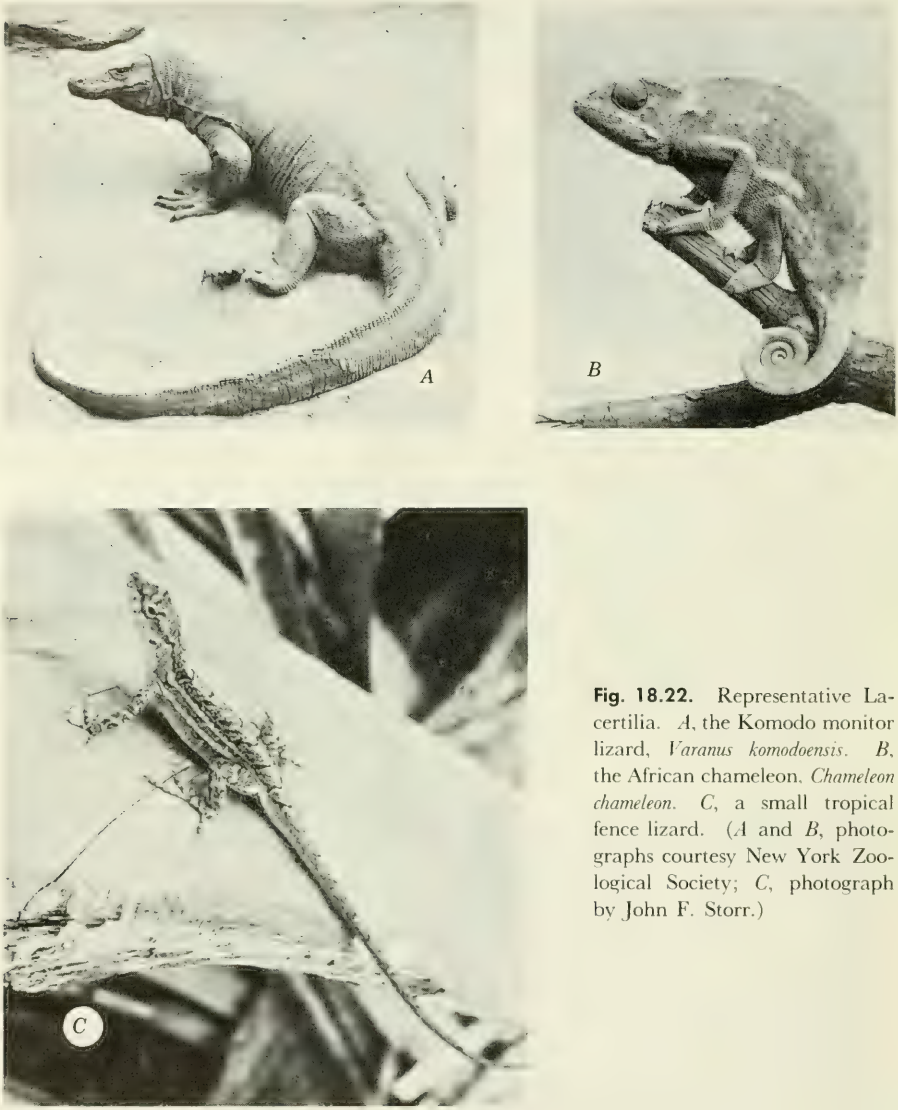


Fig. 18.22. Representative Lacertilia. *A*, the Komodo monitor lizard, *Varanus komodoensis*. *B*, the African chameleon, *Chameleon chameleon*. *C*, a small tropical fence lizard. (*A* and *B*, photographs courtesy New York Zoological Society; *C*, photograph by John F. Storr.)

The order **Crocodilia**, including alligators and crocodiles (Fig. 18.24), is represented in North America by the alligator. These, again, are reptiles that have taken to the water, although still breathing air and coming to land for egg-laying. In body form Crocodilia represent a generalized type, but in some features of their internal anatomy these reptiles are much more highly specialized than any other reptiles. This is notably true of the brain. Early representatives of Crocodilia were contemporaneous with dinosaurs and descended from the same stem among the primitive Reptilia.

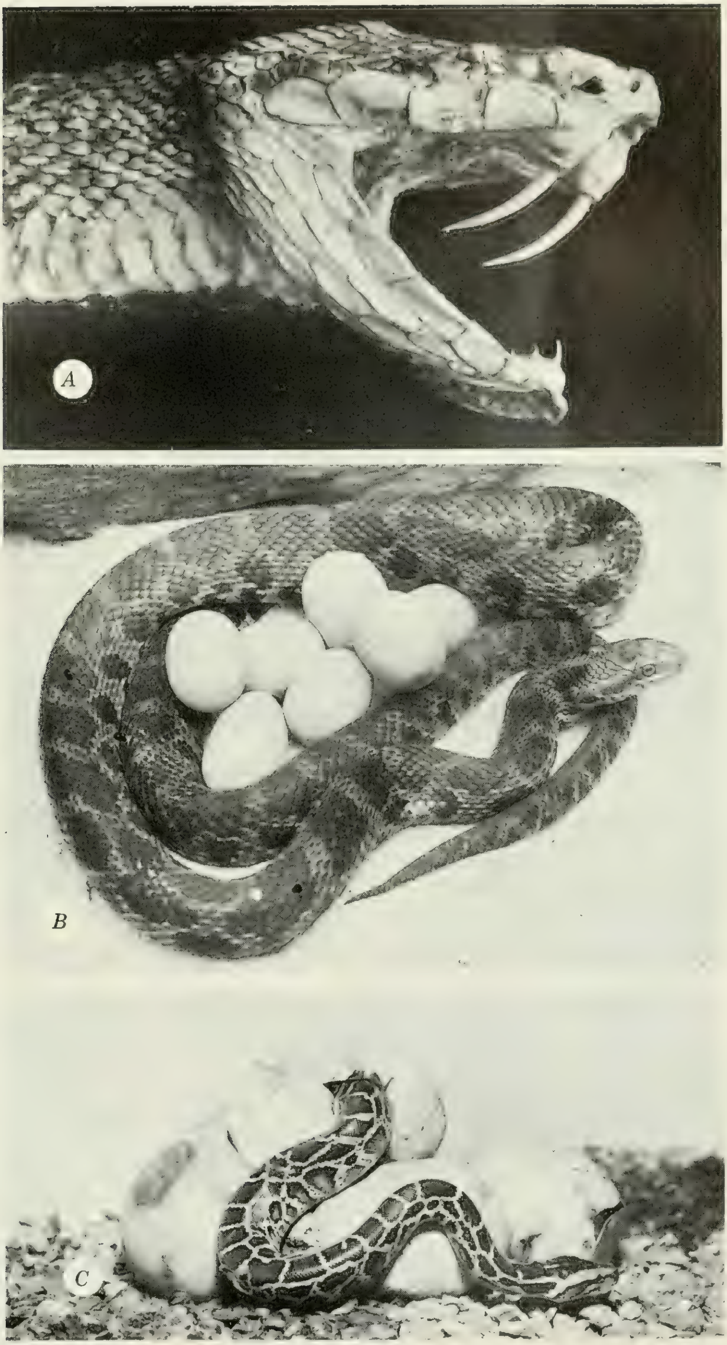


Fig. 18.23. Representative Ophidia. *A*, head of the fer-de-lance, *Bothrops atrox*, showing fangs. *B*, fox snake, *Elaphe vulpina*, with eggs. *C*, hatching young of the Indian rock python, *Python molurus*. (All photographs courtesy New York Zoological Society.)

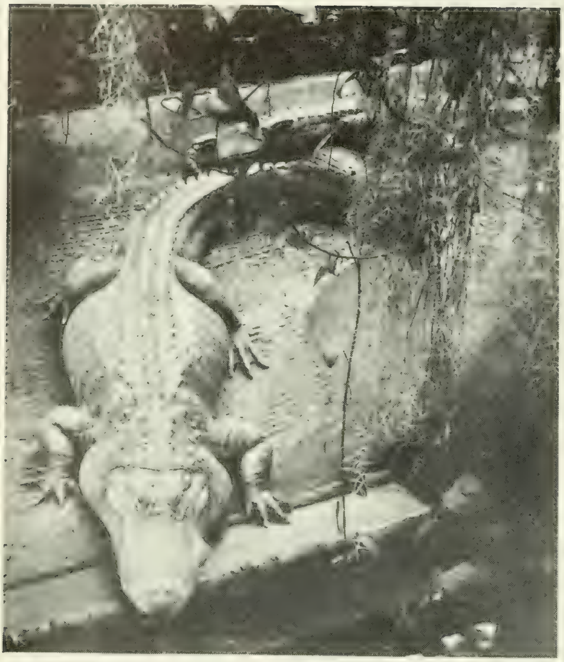


Fig. 18.24. A representative crocodilian: the American alligator, *Alligator mississippiensis*, a modern amphibious reptile. (Photograph courtesy New York Zoological Society.)

The Aves. Birds may be exactly defined as **feathered animals;** no bird is without feathers, and no other animal possesses them. In addition, birds are warm-blooded vertebrates closely resembling reptiles, from which they have obviously arisen. Among the earliest reptiles one line, from which dinosaurs and pterosaurs originated, was ancestral also to crocodiles and to birds. Toward the end of the Paleozoic or the beginning of the Mesozoic, it is probable that small reptiles of this group, already specialized for locomotion with the hind limbs, were further modified for an arboreal habitat and for flight. The nature of the earliest adaptations for flight is uncertain. The earliest known birds, now assigned to the single genus *Archaeopteryx*, whose fossils were found in the Jurassic of Germany, had feathers and presumably were moderately good fliers (Fig. 18.25). They retained, however, several reptilian characteristics which have since been lost, or much reduced, in the avian line. Among these primitive features were teeth, an elongate tail, and claws upon some of the digits of the fore limb. No other fossils of birds are known between the Jurassic and the Upper Cretaceous, when the toothed aquatic forms *Hesperornis* and *Ichthyornis* flourished. These two genera represent lines that became highly specialized for aquatic life before they became extinct. It is assumed that birds were abundant in the Upper Cretaceous, because the birds of the early Tertiary are diversified and essentially like those of today. In these modern forms the most important divergence is between the flightless birds, such as the existing emus, cassowaries, and ostriches, and

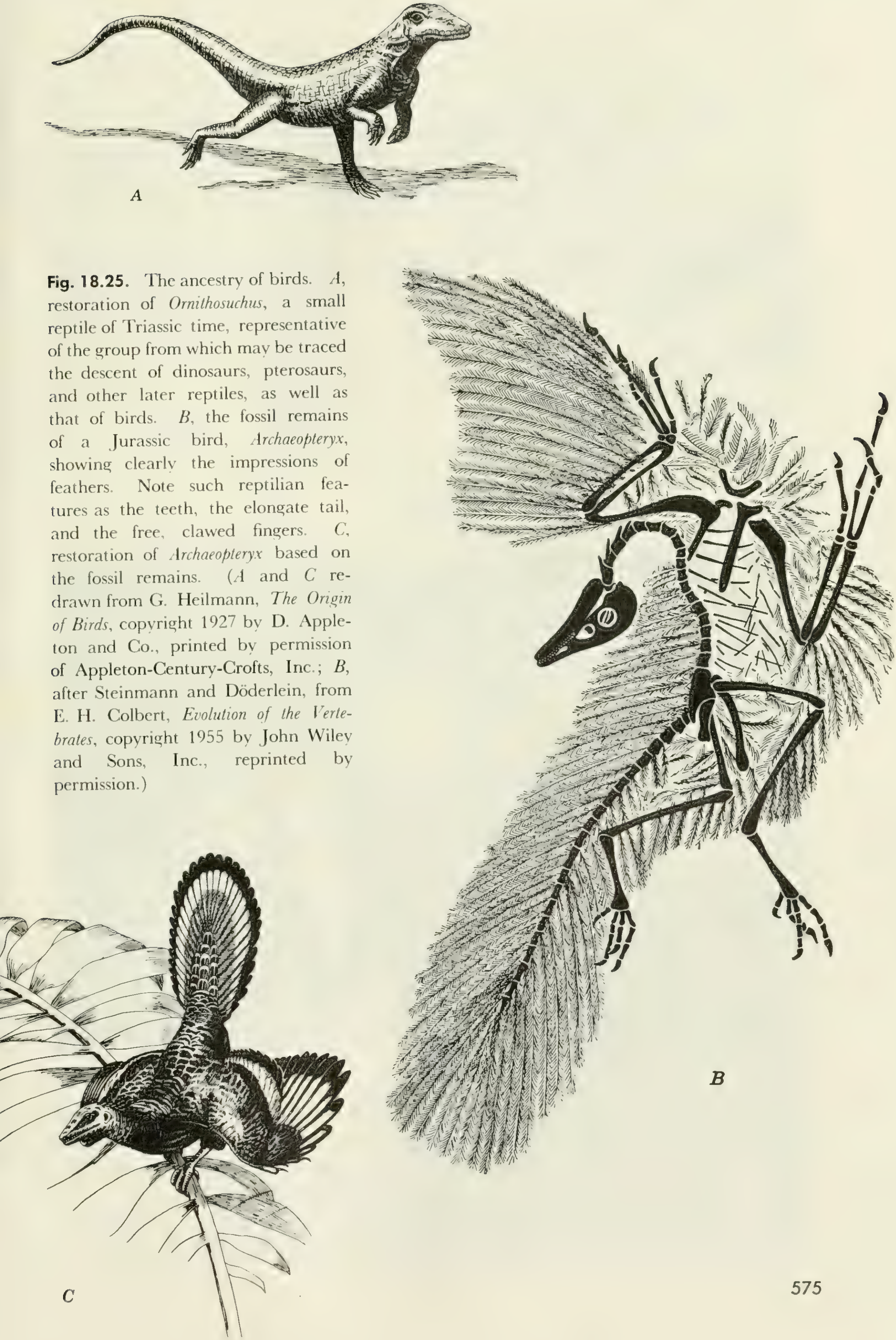


Fig. 18.25. The ancestry of birds. *A*, restoration of *Ornithosuchus*, a small reptile of Triassic time, representative of the group from which may be traced the descent of dinosaurs, pterosaurs, and other later reptiles, as well as that of birds. *B*, the fossil remains of a Jurassic bird, *Archaeopteryx*, showing clearly the impressions of feathers. Note such reptilian features as the teeth, the elongate tail, and the free, clawed fingers. *C*, restoration of *Archaeopteryx* based on the fossil remains. (*A* and *C* redrawn from G. Heilmann, *The Origin of Birds*, copyright 1927 by D. Appleton and Co., printed by permission of Appleton-Century-Crofts, Inc.; *B*, after Steinmann and Döderlein, from E. H. Colbert, *Evolution of the Vertebrates*, copyright 1955 by John Wiley and Sons, Inc., reprinted by permission.)

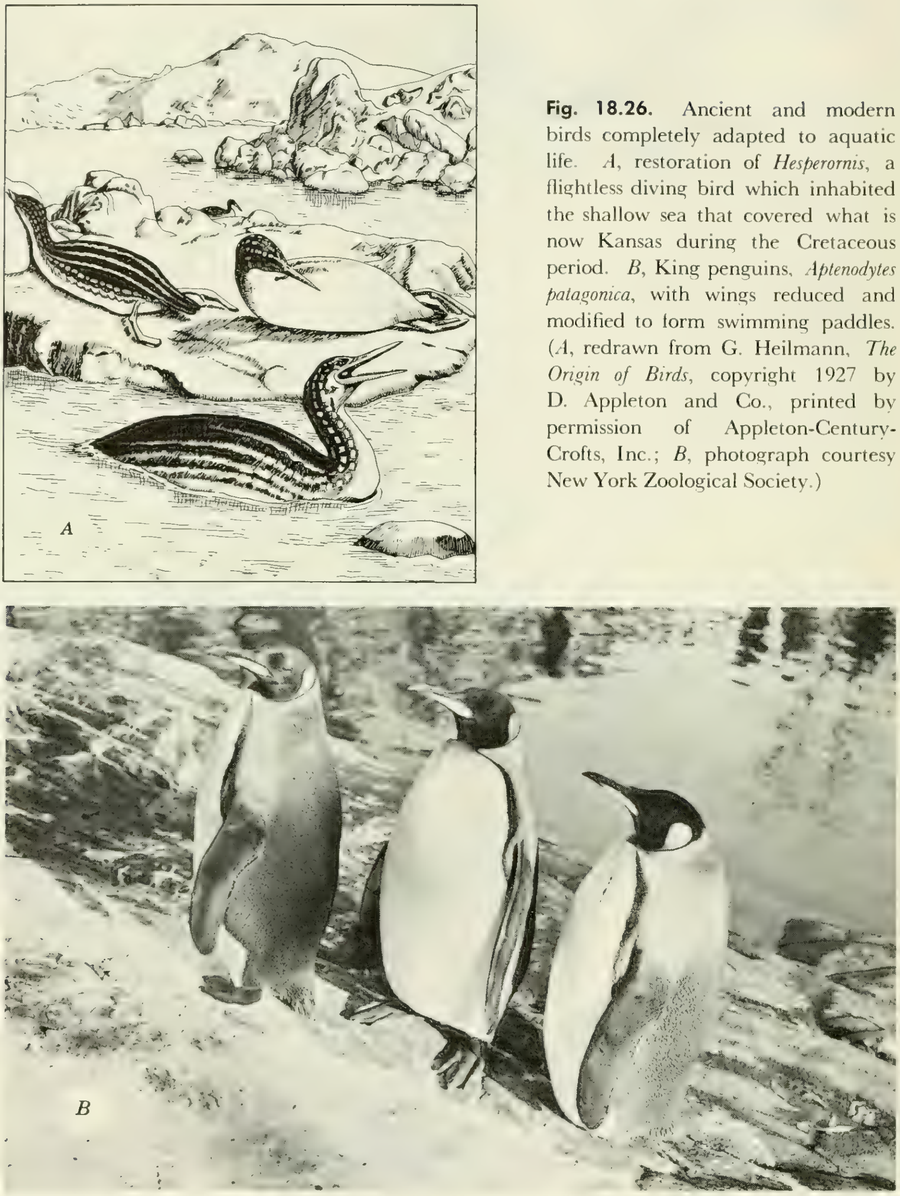


Fig. 18.26. Ancient and modern birds completely adapted to aquatic life. *A*, restoration of *Hesperornis*, a flightless diving bird which inhabited the shallow sea that covered what is now Kansas during the Cretaceous period. *B*, King penguins, *Aptenodytes patagonica*, with wings reduced and modified to form swimming paddles. (*A*, redrawn from G. Heilmann, *The Origin of Birds*, copyright 1927 by D. Appleton and Co., printed by permission of Appleton-Century-Crofts, Inc.; *B*, photograph courtesy New York Zoological Society.)

the great majority of birds which are adapted for flight. The flying birds typically have a keeled sternum for attachment of the powerful wing muscles, whereas in the cursorial or running birds the wings and flight muscles are much reduced and the sternum is without a pronounced keel.

The poverty of the fossil record of birds seems explicable by the fact that a bird, with its light body, particularly its light bones, is much less likely to leave a record as a fossil than is a heavier animal. The usual habitats and habits of birds also make it less probable that these forms would fall to earth in places where fine sediments were being rapidly deposited. More fossils of birds may be discovered at any time, but it is unlikely that their record will ever approach that of animals more commonly buried in the mud of some shallow body of water and thus fossilized.

The class **Aves** is divided into the subclass **Archaeornithes,** containing the extinct forms with teeth and other conspicuous reptilian characteristics (*Archaeopteryx*), and the subclass **Neornithes,** including in four superorders the remaining known birds, extinct and existing. The **Odontognathae** are the

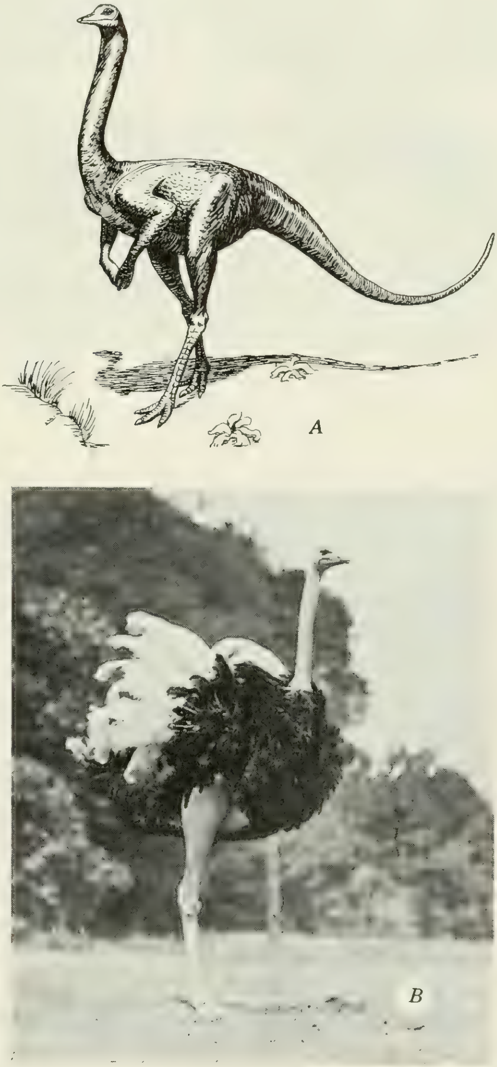


Fig. 18.27. Dinosaurs and flightless birds. *A*, *Struthiomimus*, a bipedal dinosaur of the Cretaceous. *B*, the North African ostrich, *Struthio camelus*. Many of the features of *Struthiomimus* were strikingly similar to the characteristics of modern flightless ratite birds; however, these similarities are examples of convergence in evolution, for these forms do not appear to be at all closely related. (*A*, redrawn after G. Heilmann, *The Origin of Birds*, copyright 1927 by D. Appleton and Co., printed by permission of Appleton-Century-Crofts, Inc.; *B*, photograph courtesy New York Zoological Society.)

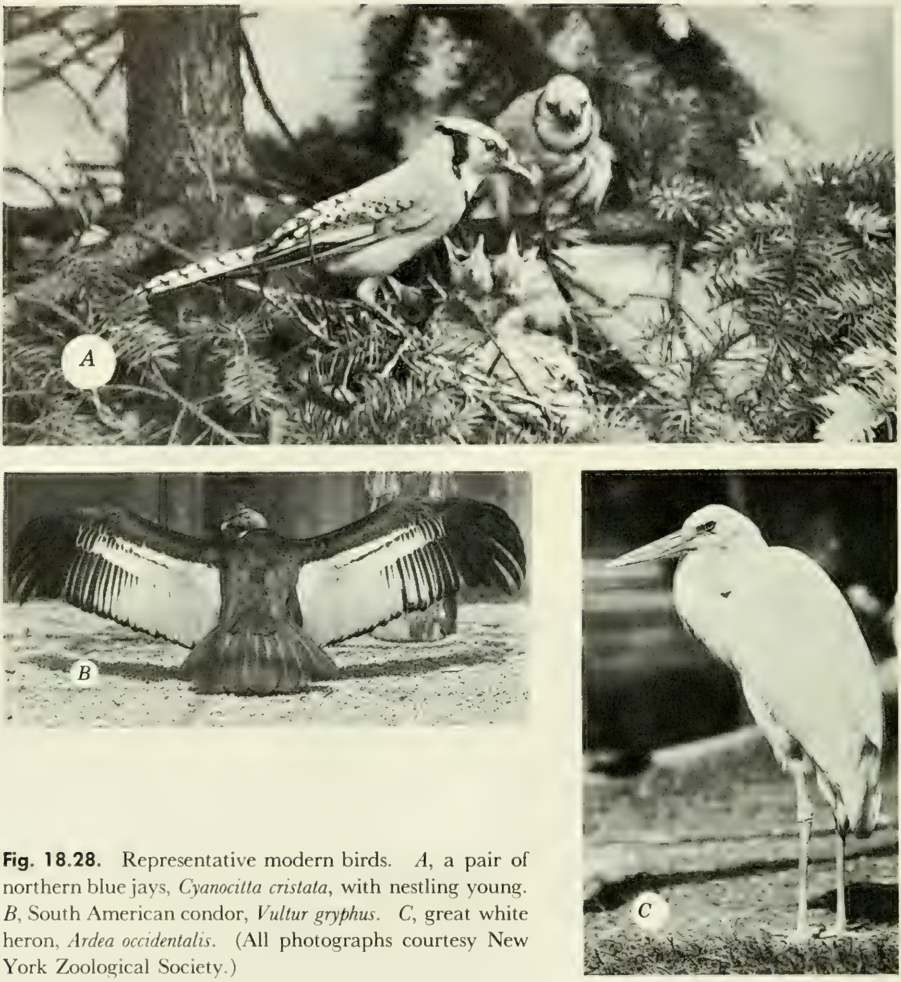


Fig. 18.28. Representative modern birds. *A*, a pair of northern blue jays, *Cyanocitta cristata*, with nestling young. *B*, South American condor, *Vultur gryphus*. *C*, great white heron, *Ardea occidentalis*. (All photographs courtesy New York Zoological Society.)

extinct aquatic, toothed birds, *Hesperornis* (Fig. 18.26) and *Ichthyornis;* the **Palaeognathae** are various flightless birds such as rheas, emus, cassowaries, ostriches, and others (Fig. 18.27); the **Impennes** are the penguins (Fig. 18.26); and the **Neognathae** include the more common and familiar birds, forming the majority of existing species (Fig. 18.28).

As we mentioned previously, a group of reptiles, the pterosaurs or pterodactyls, also evolved the power of flight, flourishing and then becoming extinct. These were contemporaneous with the primitive birds and sprang from the same reptilian line, although representing an independent offshoot. Characteristics of selective advantage, evolved by the ancestors of the birds, were their temperature-regulating ability, their nesting habit, the greater care given the young, and their feathers, which form a strong, light, and insulating covering for the body. The birds represent an advanced type of vertebrate animal which might have become dominant upon land instead of the mammals; they might even have evolved a level of intelligence comparable with that of man. Instead, the integrative mechanisms of birds, like those of insects, evolved with emphasis on instinctive, inherited behavior patterns, apparent, for example, in their nesting habits, migratory flights, and other activities.

A review of existing birds is impossible within the limits of this chapter. Despite diversity in appearance and habits, they are a homogeneous group when compared with such classes as the reptiles, living and extinct, and the mammals. The flightless birds (Palaeognathae) seem to have originated from flying ancestors, rather than from ancestors in which the power of flight had never been developed. Loss of flight in these birds may have been related to their isolation in such regions as Australia, New Zealand, and Madagascar, where there were few if any carnivorous enemies. Apparently the ability to fly has been lost in a number of independent lines of birds during the evolution of the class. Many recent birds have become modified in relation to aquatic life, although none so completely as the penguins (Impennes). Most characteristic of existing bird life are the small perching birds familiar as our common songsters.

The Mammalia. A mammal might be loosely defined as a reptile further specialized for terrestrial life. Mammals can be defined technically as vertebrates with **hair** and **mammary glands**, without specifying the less obvious characteristics by which they may be further distinguished. In intelligence they are the highest class of vertebrates, and we think of them as most advanced in complexity of structure, although birds and mammals represent comparable climaxes in vertebrate specialization. The characteristics by which mammals are better qualified than reptiles for terrestrial life are their temperature regulation, their manner of reproduction, their mechanisms of locomotion, and, by no means least, their brains. To a lesser extent their eyes, ears, and teeth seem more efficient than those of reptiles. The comparison presents the mammal as an animal more capable of going into action, maintaining action, and reproducing its kind than any of its reptilian ancestors or contemporaries.

The class **Mammalia** is subdivided into three subclasses, on the basis of clear-cut differences in reproductive habits. The subclass **Prototheria** includes the oviparous, or egg-laying, mammals: *Ornithorhynchus*, the platypus, and *Echidna*, the spiny anteater. The subclass **Metatheria**, or **Marsupialia**, contains the marsupial or pouched mammals: bandicoots, opossums, wombats, phalangers, and kangaroos. The subclass **Eutheria**, or **Placentalia**, includes the viviparous mammals, represented by all the more advanced and familiar forms. These are distributed among sixteen orders, of which the following are representative:

Order **Insectivora**: moles, shrews, and hedgehogs.
Order **Chiroptera**: bats.

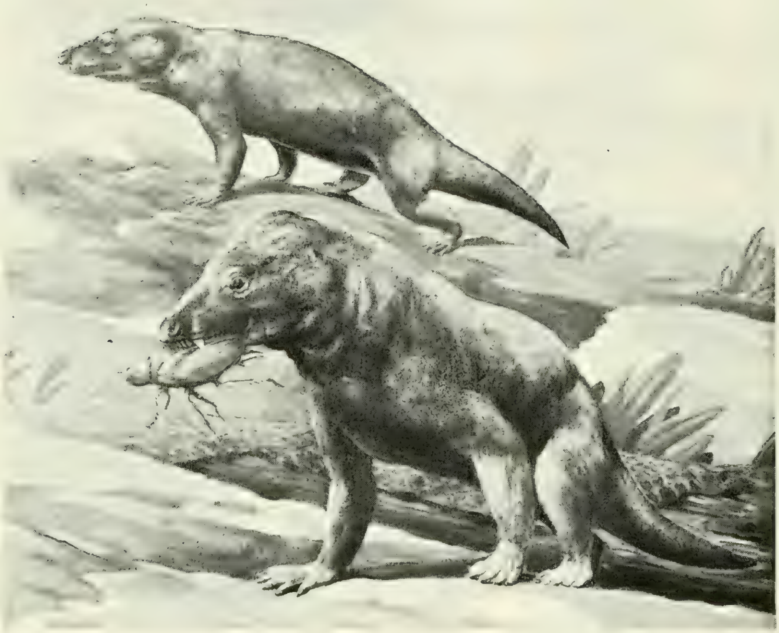


Fig. 18.29. Reconstruction of a mammal-like reptile, *Cynognathus*, which lived in late Triassic time and represents a reptilian type believed to have been ancestral to mammals. (Photograph courtesy American Museum of Natural History.)

Order **Primates**: lemurs, monkeys, apes, and man.
Order **Carnivora**: cats, lions, dogs, wolves, foxes, bears, raccoons, seals, sea lions, walruses, and many others.
Order **Perissodactyla**: odd-toed hoofed mammals, such as horses, zebras, tapirs, and rhinoceroses.
Order **Artiodactyla**: even-toed hoofed mammals, such as swine, hippopotami, camels, llamas, deer, cattle, and many others.
Order **Cetacea**: whales, dolphins, and porpoises.
Order **Proboscidea**: elephants.
Order **Rodentia**: rodents, such as squirrels, rats, mice, beavers, porcupines, and many others.
Order **Edentata**: sloths, armadillos, and anteaters.

The three subclasses **Prototheria, Metatheria,** and **Eutheria,** represented by the duckbill, the opossum, and the more common placental mammals, respectively, as well as the nature of mammalian embryonic development, should be kept in mind through the account that follows. The fossil record gives clear evidence of mammalian origins. Reptiles along the line leading to the Mammalia are found in the Carboniferous and Permian of Texas. Forms even more like mammals occur in the Permian and Triassic of South Africa, where they were the most common of all reptiles. Some of these animals, such as *Cynognathus* (Fig. 18.29), might as well be called mammals as reptiles; if it were known that they had given up the egg-laying habit, they would certainly be classified as mammals. No single genus among these fossils can be fixed as the specific ancestor of mammals, but it appears that in the African region a type of reptile gradually became modified so that it walked with its limbs more beneath the body, and hence with the body off the ground. From such members of the reptilian stock the mammals arose. One outcome of this change that may have been important was the ultimate possibility of more rapid and efficient locomotion.

How and when these animals became warm-blooded, hairy, and viviparous are matters of speculation. It has been suggested that increasing dryness of the climate, and so a drier land surface (for which there is evidence in the geologic records of the period), may have been factors of importance in

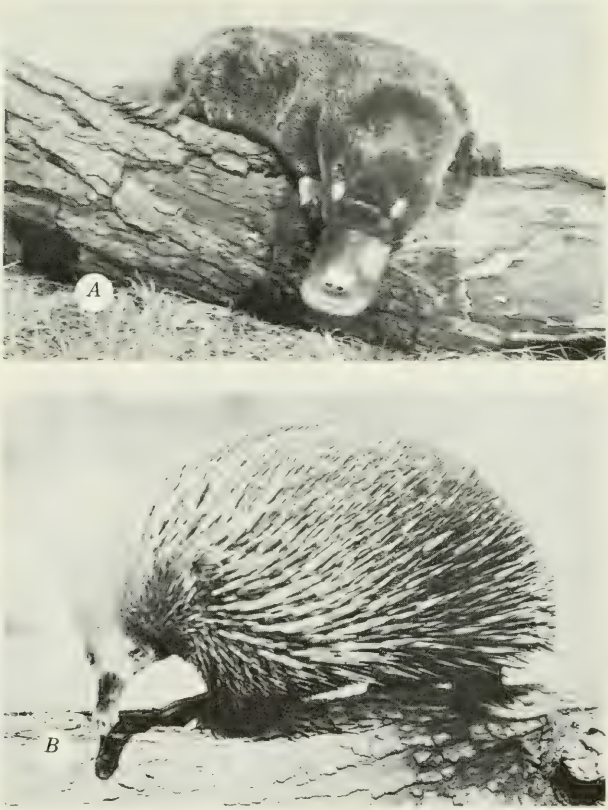


Fig. 18.30. Representative Prototheria. *A*, the platypus, *Ornithorhynchus anatinus*. *B*, *Echidna aculeata*, the spiny anteater. (Photographs courtesy New York Zoological Society.)

determining the types that survived. These reptile-mammals became extinct with the rise of the reptiles in the Mesozoic, but they seem to have left descendants that were truly mammals, and contemporaneous with the dinosaurs. Small mammals of this type, no larger than a rat, are known from fragmentary remains scattered throughout the Mesozoic. The fossils are principally jaws and teeth; not a single complete skeleton has been discovered, and not even a complete skull, until a time near the end of the Age of Reptiles. Judging from their teeth, some of these small mammals seem to have been insect eaters, and their prey probably included other small animals in addition to insects. Others had teeth indicating a herbivorous diet. It appears from a variety of evidence that they were arboreal; they may have been nocturnal, like many small mammals of today. With the reptiles so diversified and occupying the land, the water, and the air, there remained perhaps a greater degree of safety in the arboreal habitat. In any event, small mammals appear early in the Mesozoic, and they seem to have remained much as they were until the diversification of the Eutheria began near the end of this period.

Evolutionary changes have occurred not only in the adult structure of mammals, as compared with reptiles, but also in their embryonic stages. The reptilian ancestors probably laid eggs, as do modern reptiles. The Prototheria, as represented in the modern fauna by the platypus and the spiny anteater (Fig. 18.30), lay eggs somewhat resembling those of reptiles.

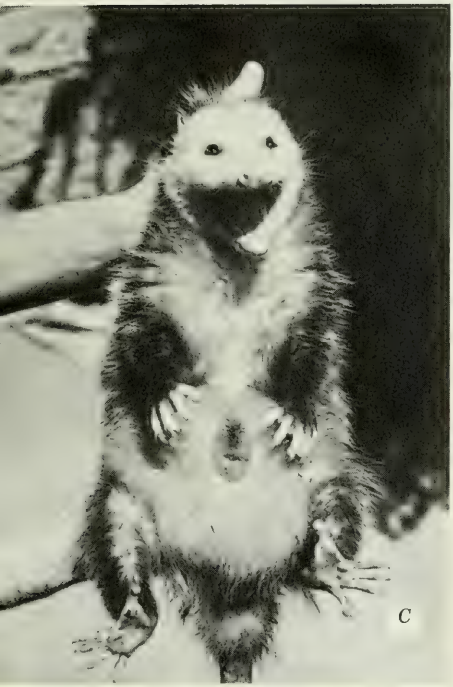
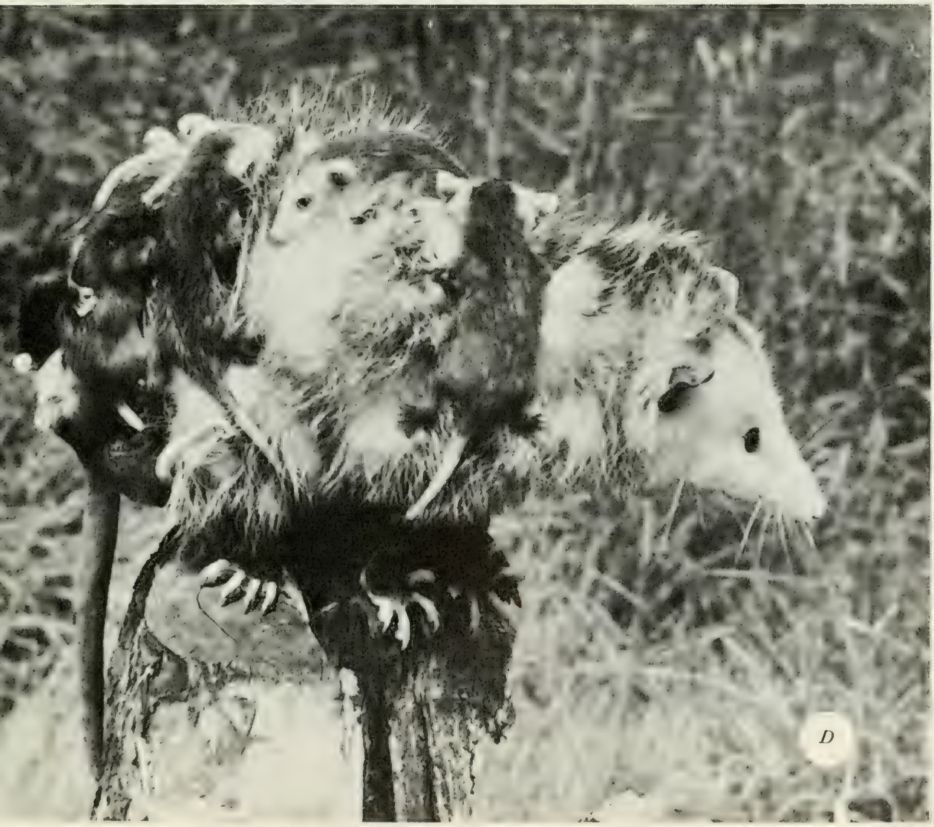


Fig. 18.31. Representative Metatheria or Marsupialia. *A*, rock wallaby, *Wallabia bicolor*, with young in marsupium. *B*, koala, *Phascolarctos cinereus*, with young. *C* and *D*, Virginia opossum, *Didelphys virginiana*, with young. In *C*, the young can be seen within the marsupium of the mother. (*A* and *B*, photographs courtesy New York Zoological Society; *C* and *D*, photographs by Charles W. Schwartz.)



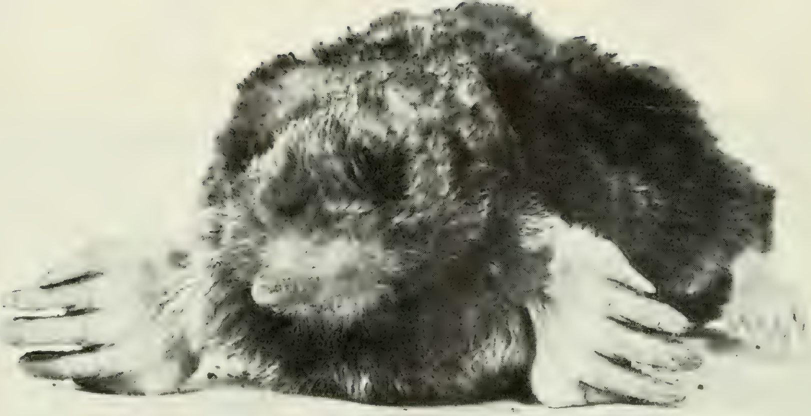


Fig. 18.32. Insectivora: the eastern mole, *Scalopus aquaticus*, strongly modified in correlation with its subterranean, burrowing habits. Note the reduction of the eyes, and the grotesque enlargement of the fore limbs. (Photograph courtesy New York Zoological Society.)

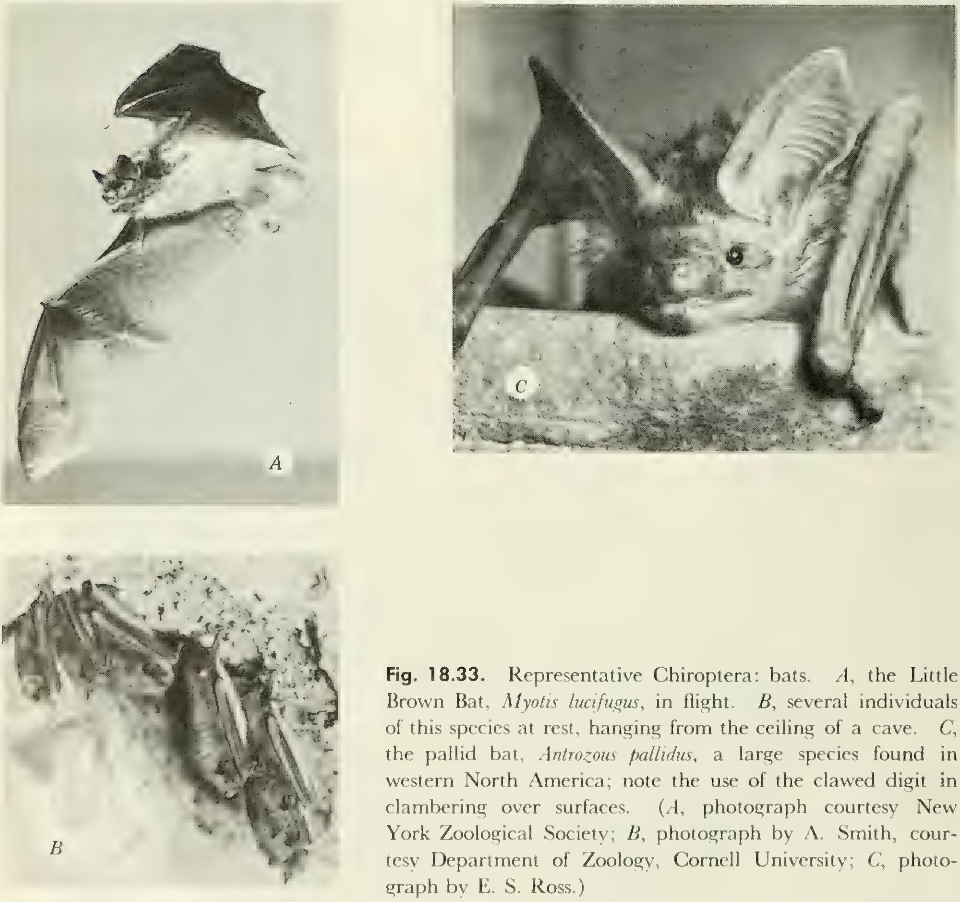


Fig. 18.33. Representative Chiroptera: bats. *A*, the Little Brown Bat, *Myotis lucifugus*, in flight. *B*, several individuals of this species at rest, hanging from the ceiling of a cave. *C*, the pallid bat, *Antrozous pallidus*, a large species found in western North America; note the use of the clawed digit in clambering over surfaces. (*A*, photograph courtesy New York Zoological Society; *B*, photograph by A. Smith, courtesy Department of Zoology, Cornell University; *C*, photograph by E. S. Ross.)

The Metatheria, such as the kangaroos and opossums, give birth to young which are minute and in a relatively undeveloped state; these young are then transferred to a brood pouch or **marsupium** until development is completed (Fig. 18.31). In the Eutheria the young are attached to the mother's uterus by the placenta and are thus nourished until they are born in more advanced stages, ranging from blind and hairless mice to colts that stand and run within a short time after birth. The Metatheria may be regarded as survivors of an evolutionary stage intermediate between the egg-laying ancestors and the

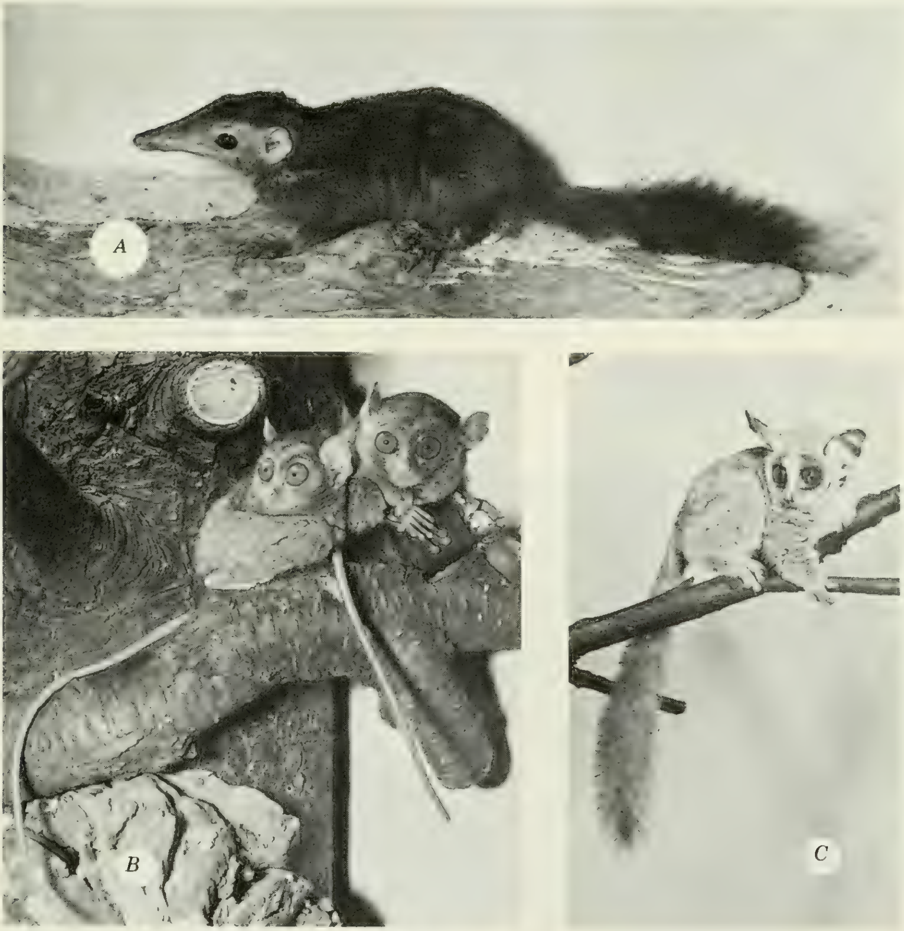


Fig. 18.34. Representative lemuroid Primates. *A*, *Tupaia*, a tree shrew; this primitive primate type exhibits characteristics which indicate the common ancestry of modern primates and insectivores. *B*, tarsiers, *Tarsius*, and *C*, a "bush baby," *Galago;* these are arboreal, nocturnal primates. The modern lemuroid primates are representatives of an evolutionary stock believed to have diverged from the anthropoid line in Paleocene-Eocene time. (Photographs courtesy New York Zoological Society.)

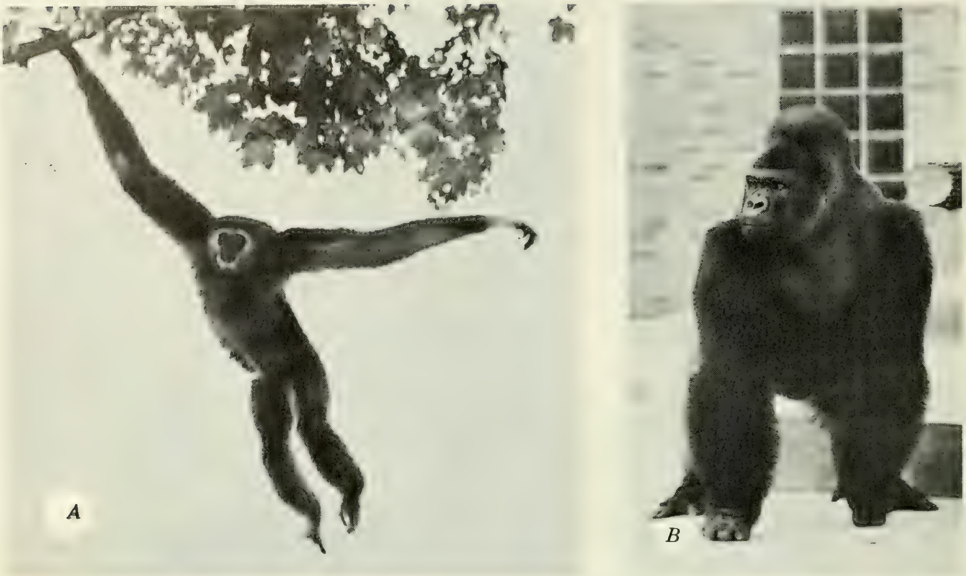
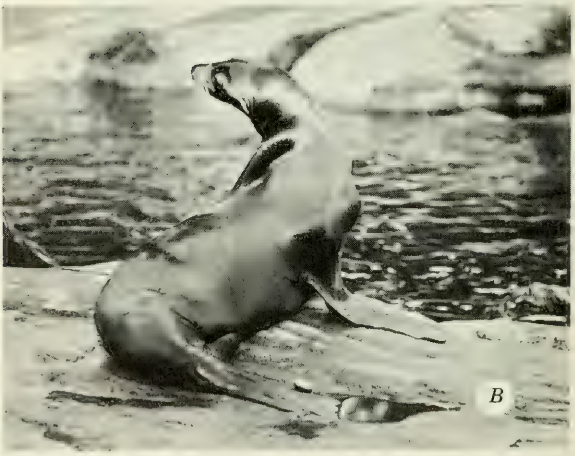


Fig. 18.35. Representative anthropoid primates. *A*, a gibbon, *Hylobates*, moving through the trees by "brachiation;" note the characteristic elongation of the arms. *B*, a gorilla, *Gorilla;* this represents a type



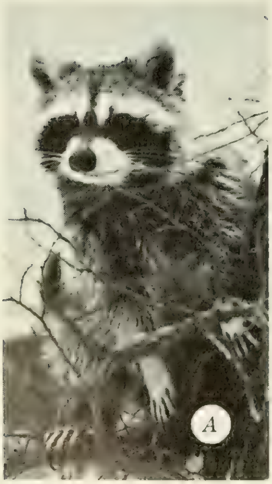


Fig. 18.36. Representative Carnivora. *A*, raccoon, *Procyon lotor*. *B*, California sea lion, *Zalophus californianus*, a carnivore highly specialized in adaptation to its aquatic way of life; *C*, young African lions, *Felis leo; D*, Canadian otter, *Lutra canadensis*. (*A*, photograph by Charles W. Schwartz; others, photographs courtesy New York Zoological Society.)

of ape which is less arboreal in its habits than most other anthropoids. *C*, orangutan, *Pongo*, and chimpanzee, *Pan*. (Photographs courtesy New York Zoological Society.)

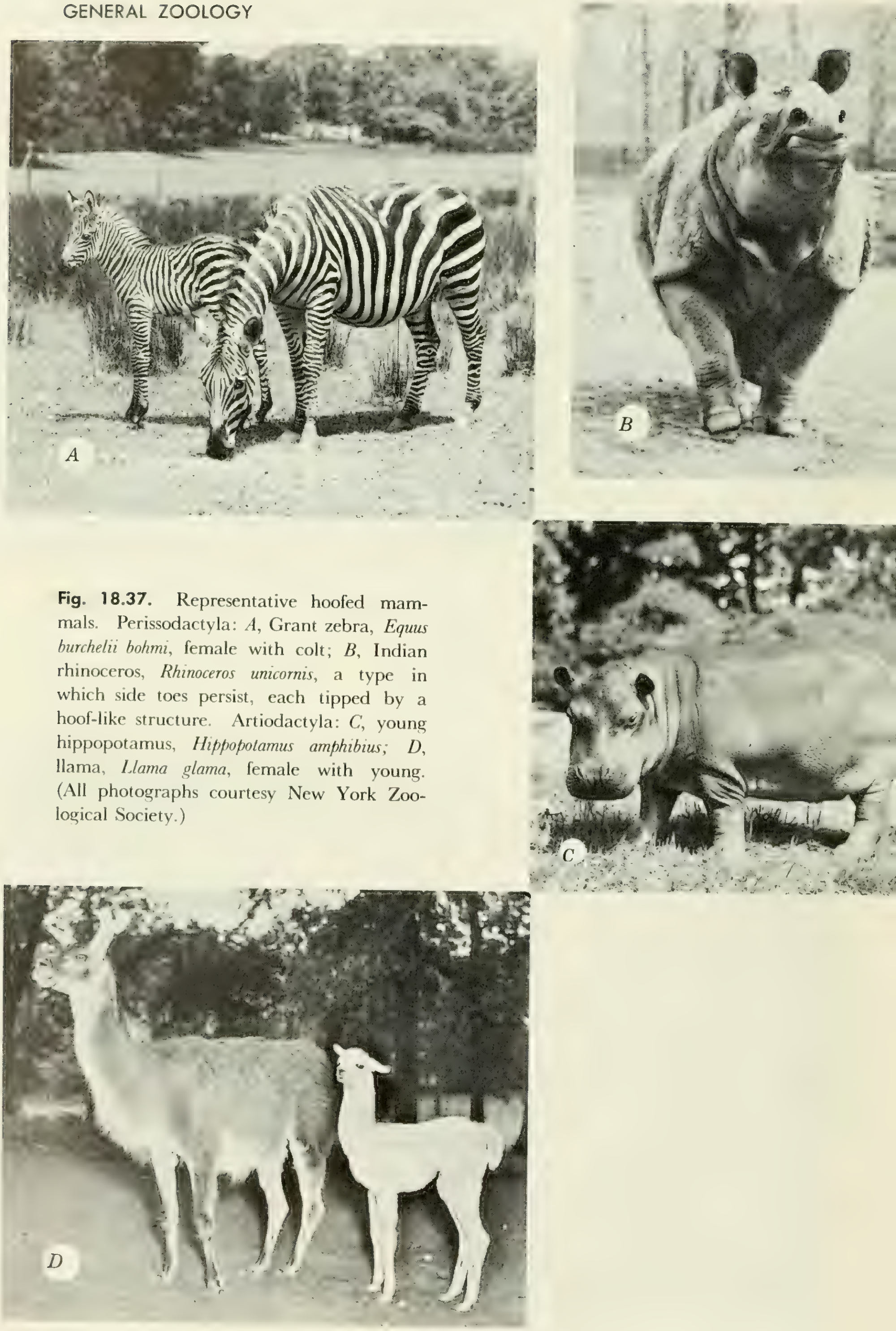


Fig. 18.37. Representative hoofed mammals. Perissodactyla: *A*, Grant zebra, *Equus burchelii bohmi*, female with colt; *B*, Indian rhinoceros, *Rhinoceros unicornis*, a type in which side toes persist, each tipped by a hoof-like structure. Artiodactyla: *C*, young hippopotamus, *Hippopotamus amphibius;* *D*, llama, *Llama glama*, female with young. (All photographs courtesy New York Zoological Society.)

placental mammals, although they are not ancestral to these mammals. Study of mammalian and reptilian embryos shows that the embryonic membranes of the mammal so closely resemble those of the reptile and bird that they must have been derived from the reptilian source. There is no yolk in the egg of a placental mammal, but a yolk sac forms during development (p. 162).

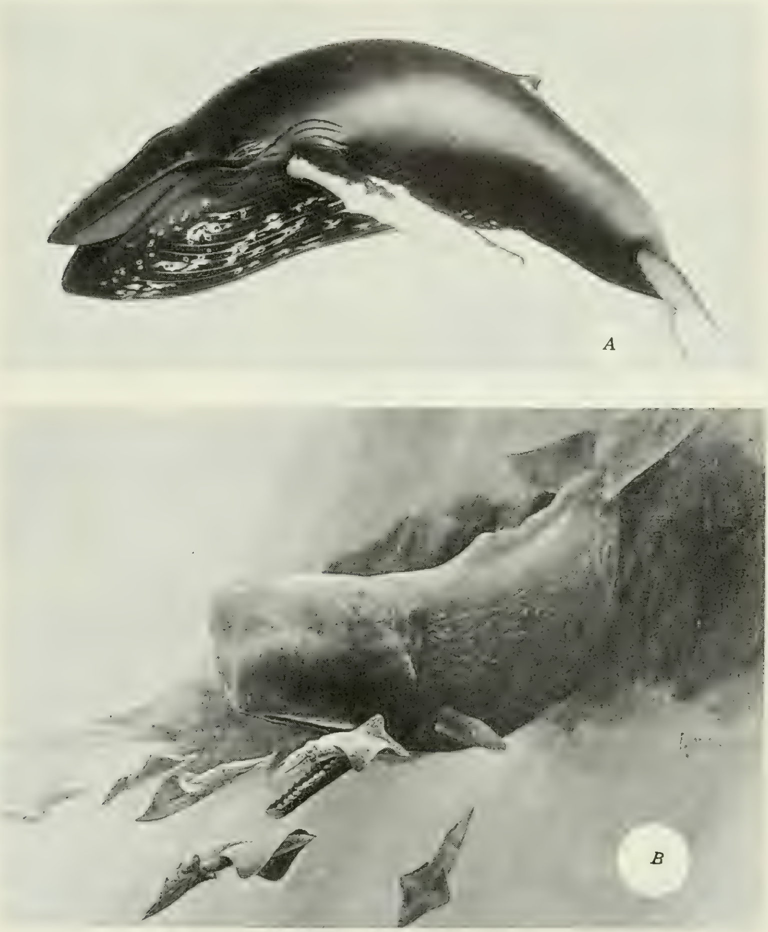


Fig. 18.38. Representative Cetacea. *A*, hump-backed whale, *Megaptera nodosa;* this is a "whalebone whale," feeding with the aid of plates of baleen suspended from the upper jaw. *B*, sperm whale, *Physeter*, one of the toothed whales, pursuing the squid which form the greater share of its food. The structural adaptations to marine life in these mammals may be compared with those of fishes, ancient marine reptiles, and modern marine Carnivora such as seals and sea lions. (*A*, photograph of a model; *B*, photograph of a painting by F. L. Jacques; both courtesy American Museum of Natural History.)

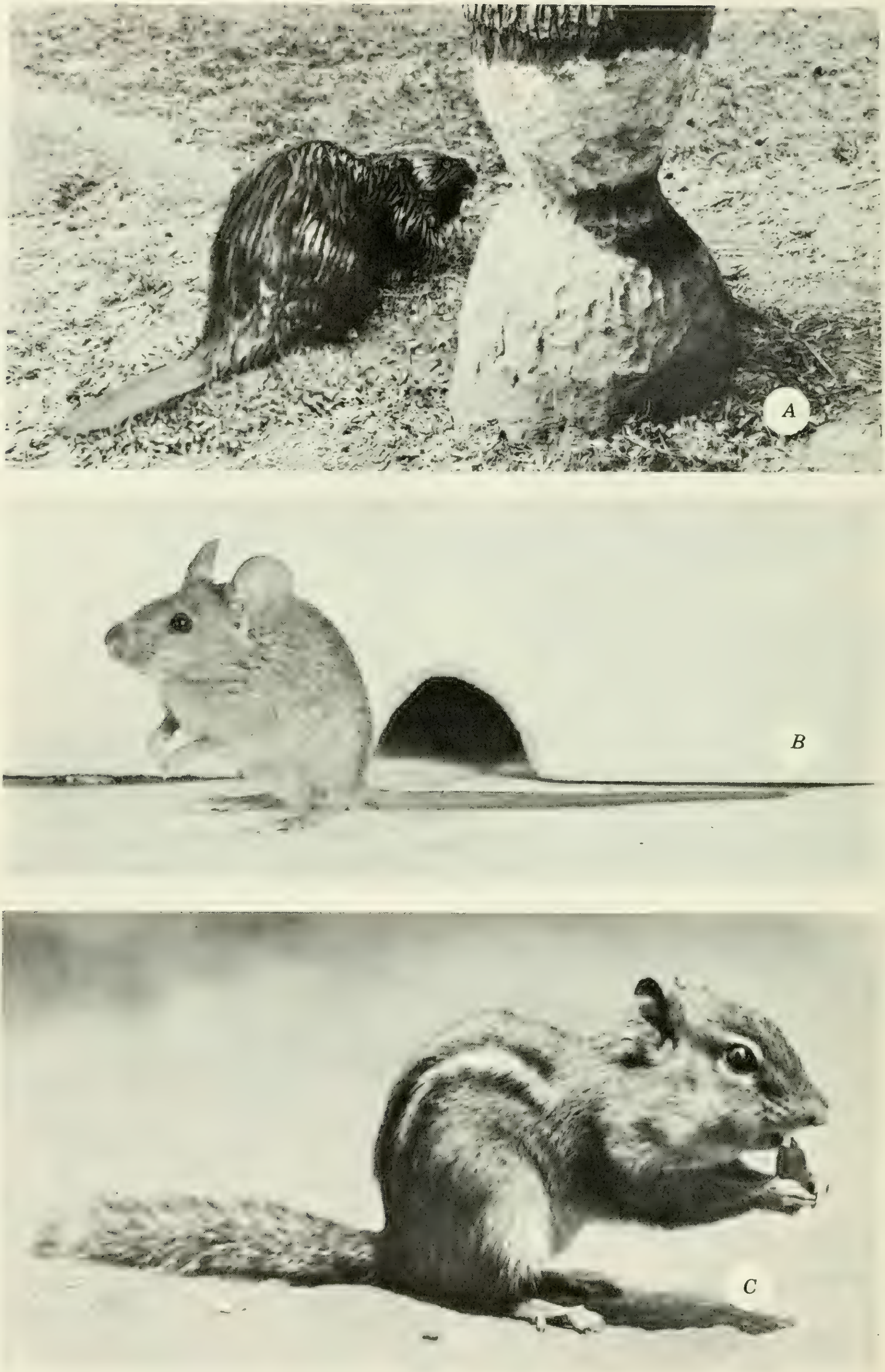


Fig. 18.39. Representative Rodentia. *A*, beaver, *Castor canadensis*, and a tree showing the work of the animal's chisel-like incisor teeth. *B*, the house mouse, *Mus musculus*. *C*, eastern chipmunk, *Tamias striatus*. (Photographs courtesy New York Zoological Society.)

Thus, mammals of small size were present as an insignificant fraction of the population during the millions of years that witnessed the rise and dominance of dinosaurs and other ruling reptiles and the rise of birds. The fossil record is incomplete; but if there had been many larger species of mammals, some would certainly have been preserved as fossils and found before this. Only toward the close of the Mesozoic, which marks the end of the Age of Reptiles, did the diversification of the mammals begin. In the Age of Mammals, when this class of warm-blooded vertebrates became dominant upon the land, they seem to have replaced reptiles by an expansion into territory that was being relinquished. The mammals were the more efficient of the two; they had warm blood, which enabled them to range at will, and greater possibilities of locomotion, to say nothing of wits. What seems to have happened is not that the more efficient type drove out the less efficient but that the reptiles declined for some unknown reason, and so the land again became free for new occupants. The mammals were at hand and became the dominant land forms of the Tertiary, or Age of Mammals, as the early amphibians and reptiles had become dominant upon the older land surfaces. The early mammals were small insect eaters, but diversification into the principal mammalian types was rapid, and with increase in size of the individuals in many lines the great mammalian fauna of the Tertiary came into being. Like the fishes, amphibians, and reptiles, the mammals had their day; they were a waning race even before many recent forms were confronted with ultimate extinction through the activities of *Homo sapiens*. Representative types of existing mammals are shown in Figures 18.30–18.39.

Along with that of other mammals, the human line of descent begins with the insect eaters of the trees at the close of the Age of Reptiles. Surviving offshoots that mark the path of this evolution are the existing lemurs, tarsiers, monkeys, and great apes; this descent is confirmed by what is known from fossils. Only in the late Tertiary or earliest Pleistocene, it seems, did our ancestors descend from the trees; binocular vision and important qualities of hand and brain, along with the beginnings of an upright posture, were established before man's forebears came to earth. The later phases of human evolution are outlined in Chapter 20. Speaking of our ancestors in the early Tertiary, W. D. Matthew describes their appearance as intermediate between that of a lemur and a mongoose. They were animals "rather catholic in their tastes, living among and partly in the trees, with a sharp nose, bright eyes and a shrewd little brain behind them, looking out, if you will, from a perch among the branches, upon a world that was to be singularly kind to them and their descendants."

Summary

The phylum Chordata includes certain invertebrate animals along with the familiar vertebrates. The species representing the lowly members of the phylum are few in number and superficially unlike their numerous vertebrate relatives. Yet they have the gill slits, notochord, and nervous system of the chordate. Since vertebrates appear as fishes in the Ordovician, it is concluded that these first vertebrates of the fossil record must have been preceded by fairly complex ancestors in the Cambrian, in which representatives of all the other major phyla are found. This means that a common ancestor for all chordates would be sought in the Age of Invertebrates. No fossils representing such an ancestor are available, and it is unlikely that any will ever be found. The origin of vertebrates from some invertebrate source was the subject of much speculation, based on the data of comparative anatomy and embryology, when such theorizing was the vogue in the last decades of the nineteenth century; nothing that proved convincing was ever made of the matter, and it is unlikely that anything ever will be. The animal life of the Cambrian is remote, but it was preceded by millions of years from which we have virtually no fossils and during which the Cambrian types were evolved. In studying evolutionary history within the subphylum Vertebrata, we have access to the fossil record and also to "surviving fossils," such as the egg-laying mammals, whose structure and development can be fully examined. Reconstructing the past from the data available, we conclude that the earliest vertebrates were small, heavily armored, bottom-dwelling, fish-like animals, living in fresh water rather than the salt water from which their remote ancestors presumably came. From such early fishes came others that made a beginning of air-breathing while still in fresh water, and some of these invaded the ocean. Late in this Age of Fishes came the first land vertebrates, the Amphibia, descended from the air-breathing fishes known as lobe fins. In the Age of Amphibians, when the great coal measures were being laid down, these vertebrates were the dominant forms upon the marshy land surface. Reptiles arose from early amphibians and succeeded them in the Age of Reptiles. Both birds and mammals appeared as early offshoots from reptilian lines; the mammals remained small and insignificant animals until the reptiles began to decline. In the Age of Mammals the members of this class were able to range more widely than any of their predecessors, because of their effective locomotion, their warm-bloodedness, and their mode of development within the parent. As the mammals declined toward the end of the Tertiary, the human stock became differentiated from other Primates; the present is sometimes called the Age of Man.

CHAPTER 19

CHAPTER 19

ECOLOGY:
Environmental Relationships

The characteristics of an animal, and the range of activities of which it is capable, are largely determined by its genes; these represent the material of inheritance, or heredity. It is clear, however, that although an animal comes into being with a specific hereditary endowment, the expression of its inherent characteristics is conditioned at all levels by intrinsic and extrinsic factors which collectively may be termed its **environment.** What an animal is, therefore, depends on the complex interaction of hereditary and environmental factors. The study of heredity, discussed at length in Chapter 6, forms the subject matter of the field of genetics; the environmental relationships of organisms are the concern of the field of ecology, using the term in its broadest sense. At the molecular, cellular, and organismal levels, various aspects of the **internal environment** of the cells and tissues of the individual are studied by the biochemist, the cytologist, and the physiologist; the ecologist deals with the interrelationship between the organism and its **external environment.**

The external environment consists of every factor in the habitat which in any way, directly or indirectly, affects the organism. Animals are dependent on the external environment in a great many ways. Among other things, the environment furnishes a substrate for support and locomotion, a medium for gaseous exchange, and food materials for the growth, maintenance, and repair of the living organism. A great many environments, tremendously varied, have proved themselves capable of supplying these needs to various groups of animals: oceans, lakes, ponds, and streams; hot and cold springs; arctic, temperate, and tropical land masses; dung heaps, fallen logs, the bodies of plants and other animals; and so on. Each of these environments may be thought of as a composite of what we call **physicochemical** factors, such as temperature, oxygen, light, and others; and **biotic**

Fig. 19.1. Effects of different constant temperatures on the pupal stage of the fruit fly, *Drosophila melanogaster.* The figures are means of values obtained separately for male and female flies in the original experiments. (Adapted from D. Ludwig and R. M. Cable, 1933, *Physiological Zoology,* vol. 6.)

Temperature (°C.)	Duration of Pupal Stage (Days)		Percentage of Flies Emerging	
10	—		0	
15	13.8		96	
20	6.6		97	
22.5	5.1		99	Apparent optimum
25	4.1		98	
26	3.9		100	
27.5	3.5	Apparent optimum	99	
30	3.2		96	
32	3.4		78	
33	3.5		39	
34	—		0	

factors, those for which all the organisms living together in the environment are responsible. Every individual inhabiting a particular environmental situation exerts effects on its surroundings and on other organisms and thus constitutes a factor in their environment. Ecology has been defined as the study of the action of the environment on the organism, and the reaction of the organism on the environment. In seeking to elucidate the complex interrelationships implicit in such a definition, students of ecology have developed the field into a broad and very active area of investigation.

The environmental relationships of organisms have interested observers since the beginnings of biological science; the work of early naturalists and systematists, and much of the field of "natural history" in later years, formed the foundation of the modern science of ecology. It has been said, indeed, that ecology is "scientific natural history," which has developed from the older observational science by the application of experimental methods and rigorous quantitative treatment to recognized problems. Modern ecology makes use of the techniques of chemistry, physics, analytical and statistical mathematics, population genetics, and other highly specialized fields, in addition to the more general methods of biology. The importance of ecological studies cannot be overemphasized. Like all scientific work, they increase our knowledge of the world about us. In addition, these studies make it possible to plan intelligently the proper utilization and conservation of natural resources, and to predict the probable consequences of current practices in the many areas in which human activities come into contact, and often interfere, with the environment.

It is a common observation, and it is evident from much that has been said in previous chapters, that animals are well adjusted to the environments in which they occur. It might better be said that animals are found in environments in which the prevailing conditions make it possible for them to survive and to reproduce. The maintenance of this harmony between organism and environment, as well as the clearly adaptive nature of the differences between related organisms living in different environments, indicates that adaptation to environmental conditions must have played a major role in the evolution of animals. The evaluation of this role of the environment as a conditioning or guiding factor in evolution has been of great significance in the development of theories of evolution, to be discussed in Chapter 20. In the present chapter we shall consider some of the general principles that have emerged from studies of the environmental relationships of existing animals—principles illustrating the significance of environmental factors in determining the survival and distribution of animals.

The Physicochemical Environment

The physicochemical environment is a composite of a great many physical and chemical factors, any one of which may be of primary importance in determining the suitability or unsuitability of a particular environment for a specific type of organism. Although any organism is always exposed to many of these factors simultaneously, it is instructive, and indeed often necessary, to isolate the effects of a few of them individually in order to understand how they limit the activities and distribution of living things.

Temperature. It is probable that temperature affects animals more conspicuously, and in more different ways, than any other environmental factor. Temperatures vary widely, in different geographical locations, at different depths or altitudes, and even in the same localities at different times of the day or seasons of the year. Changes in temperature exert marked effects on the metabolic rates and activities of animals, as well as on their processes of growth and reproduction.

The metabolic processes of animals are fundamentally chemical reactions, and the rates at which these reactions proceed are determined by the temperature of the living system. The majority of animals are dependent for the maintenance of their body temperatures on heat from the external environment (i.e., are **ectothermous** or "cold-blooded"); therefore, the rates of their metabolic reactions are determined by the temperature of the environment. With lowered temperature there is a progressive decrease in metabolic rate, to a point at which dormancy ensues and metabolism is barely detectable. At still lower temperatures, below 0°C., the fluids of the body eventually freeze and the animal usually dies. There is great variability between different species of ectothermous animals in the degree of resistance to low temperatures. Some insects, for example, living usually at more normal temperatures, can remain in a cold-induced dormancy for long periods and can even withstand freezing. Others die after a few hours or days of exposure to intense cold. On the other hand, there are many species of cold-blooded animals which become active and thrive only at temperatures much too low to sustain metabolism in other forms.

With rising temperatures, ectothermous animals become more active; their metabolic rates increase, and they "live faster." At a certain point, however, again varying between different species, continued increase in temperature begins to affect the animal adversely. Eventually, a heat-induced dormancy supervenes, followed very soon by the death of the animal. The maximum temperatures that even the most heat-resistant species can withstand appear to lie between 48 and 52°C.; most animals are killed by considerably lower temperatures. The primary effect of heat is a derangement of the delicately balanced physical state of cellular constituents, probably through minute changes in proteins and lipids.

For every species of ectothermous animal, there is thus a specific range of temperature within which the organism remains active and capable of carrying on its vital functions. Within this range, between the maximum and minimum tolerable temperatures, there is a narrower zone at which the animal operates with greatest efficiency; this is its **optimum** temperature. Some difficulty is often experienced in precisely defining the optimum temperature; it may vary between stages in the life cycle, and, as indicated in Figure 19.1, it may differ slightly depending on the criteria used. From the standpoint of the most rapid development, the optimum temperature for the pupal stage of *Drosophila* ranges from 27.5 to 33°C.; however, this temperature range is evidently slightly above the optimum judged by the number of flies successfully completing the pupal stage. From this latter standpoint, the optimum temperature range extends from 22.5 to 27.5°C., but here development proceeds somewhat more slowly. The adverse effects of temperatures even slightly above the optimum, however defined, are evident from the data presented.

For a given species the temperature range may be extensive, or it may be restricted. Again, the range may cover only a few degrees near zero; it may lie, for example, between 20 and 30°C.; or it may be much nearer, or even beyond, the temperature at which most other animals are killed by heat. For any species the temperature range and the optimum temperature can be determined only by observation and experimentation. We may draw the general conclusion, however, that animals with restricted temperature ranges will be found in nature in the relatively few environments where their temperature tolerances are never exceeded; but species with broader temperature ranges are likely to be much more widely distributed. Thus, temperature acts as a very significant factor in determining the survival and distribution of ectothermous animals.

By various special activities and characteristics, many kinds of ectothermous animals are able to maintain fairly constant body temperatures through a wide range of external temperature conditions. Notable among these are such insects as wasps and honeybees and such reptiles as lizards. This primitive temperature regulation is of limited significance, however, and can usually be maintained only for short periods of time. The capacity to regulate body temperature by the use of heat derived from metabolic activities, more or less independently of temperature in the external environment, is developed to its highest point in the vertebrate classes Aves and Mammalia, which are said to be **endothermous** or "warm-blooded." In these forms the body temperature is maintained at a generally favorable level for the species, despite changes in the environmental temperature. The original development of endothermy by the ancestors of modern birds and mammals was undoubtedly correlated with the perfection of hair and feathers as insulating materials, but more deep-seated physiological mechanisms are also involved. Mammals, for example, rapidly adapt to changing temperatures by complex compensatory reactions involving the breathing mechanism, heart and circulation, skin, and endocrine control of metabolism, integrated by the central nervous system (see p. 125). Long-term anatomical and physiological adaptations are common in mammals habitually exposed to low or to high temperatures. Mammals of the arctic regions have thick fur and heavy, continuous blankets of subcutaneous adipose tissue, and heat loss through radiation is often minimized by reduction of such appendages as external ears. In contrast, mammals of the warmer temperate zones, and particularly of the tropics, generally have less dense fur, lack continuous subcutaneous fat deposits, and may have large, fan-like ears which function effectively to enhance cooling through radiation (Fig. 19.2). In any environment marked by unfavorable extremes of temperature, endothermous animals frequently display adaptive behavior patterns, involving hibernation, estivation, migration, retreat to shelter, and so on, which enable them to avoid excessive exposure.

The capacity for endothermous temperature regulation makes possible, for birds and mammals, existence under a wider range of external temperature conditions than is true of any other vertebrate group. Although mammalian and avian species are structurally and functionally adapted to life between customary maxima and minima of temperature, they are not so seriously or so rapidly affected as most amphibians or reptiles would be by external temperature changes. The compensatory reactions of endothermous forms are not without limits and are not perfect; therefore, even mammals and birds are to a considerable extent dependent on favorable environmental temperatures. In man, for example, the temperature of the extremities is often several degrees below the deep body temperature; it is well known that humans may freeze to death, or under other circumstances may suffer heat exhaustion or sunstroke.

The indirect effects of temperature acting through other physical factors may be as significant to animals as the more direct effects on metabolism and other vital functions. Notable in this connection is the fact that the solubility of oxygen in water decreases markedly with increasing temperature. The exclusion of an aquatic species from waters above a certain temperature might actually be an effect of oxygen deficiency, rather than a direct temperature effect. Similarly, the ability of the atmosphere to hold water vapor in suspension changes as the temperature changes. In general, a warm atmosphere is less easily saturated with water vapor than a cold one; that is, at a given relative humidity, expressed as a percentage of complete saturation, a warm atmosphere holds more moisture than a colder one. Thus, an apparent direct effect of temperature on the survival of a terrestrial animal might actually reflect the action of temperature in altering the atmospheric humidity. It is clear, therefore, that experiments to test the effects of temperature on organisms must be planned, and the results interpreted, with attention to the indirect effects of temperature acting through other environmental factors.

Oxygen. The availability of oxygen is of obvious significance in determining the survival and distribution of animals. In an overwhelming majority of species cellular metabolism and energy release depend on a series of reactions, the ultimate step of which involves the combination of carbon with oxygen to form carbon dioxide. In the absence of adequate amounts of free oxygen, the aerobic phase of cellular metabolism is impossible. The external environment is the source of oxygen for the animal, and we have previously noted (pp. 516–517) the variety of structural and functional adaptations perfected in animals for the abstraction of oxygen from the environment, in the process of gas exchange. Only a relatively few species of animals, notably saprozoic free-living protozoans and a number of intestinal parasites among the Metazoa, can live by anaerobic metabolism in the absence of free oxygen. Metabolism in these forms is a process comparable with the anaerobic phase of metabolism in aerobic organisms. Many species appear to be "obligate anaerobes" which cannot survive in the presence of free oxygen; others utilize such small amounts of oxygen as may be present but are not dependent on it.

Some natural waters, such as the bottom layers of deep lakes, and waters rich in decaying organic matter, contain no free oxygen and are thus suitable only for anaerobic organisms. In other aquatic situations the percentage of

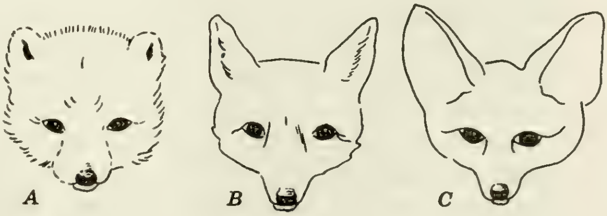


Fig. 19.2. Comparison of the heads of foxes from different climatic regions. *A*, arctic fox, *Canis lagopus;* *B*, red fox, *Canis vulpes*, of temperate regions; *C*, desert fox, *Canis zerda*. (Redrawn from R. Hesse, W. C. Allee, and K. P. Schmidt, *Ecological Animal Geography*, second edition, copyright 1951 by John Wiley and Sons, Inc., printed by permission.)

dissolved oxygen varies, being affected by temperature, degree of agitation, presence of photosynthetic plants, salt content, and other factors. As with temperature, different species of aquatic animals are commonly adapted to specific ranges of oxygen concentration, between tolerable maxima and minima, and are limited to environments where these favorable conditions obtain. Under normal circumstances, disregarding anaerobic forms, a species is more likely to be limited in its distribution by lack of oxygen than by an excess of oxygen.

Air-breathing animals, whether terrestrial or aquatic, are rarely subjected to significant variations in the amount of free oxygen for breathing. The oxygen content of atmospheric air is remarkably constant over the surface of the earth at all altitudes normally supporting animal life. There may be slight temporary or local variations—for example, near active volcanoes or in extensive industrial areas—but air normally contains about 21 per cent oxygen. This percentage does not change appreciably with increasing altitude, yet it is common knowledge that man, for example, cannot survive for any length of time under normal conditions at altitudes much above 20,000 feet. The explanation of this seeming paradox demonstrates the effect of barometric pressure on the availability of atmospheric oxygen. The respiratory exchange mechanisms of man and other mammals are physiologically adjusted to extract oxygen from air at barometric pressures characteristic of sea level, about 760 mm of mercury. With increasing altitude, barometric pressure steadily decreases, with a consequent decrease in the density of the air. At 18,000 feet, for example, barometric pressure is approximately half the sea-level value; here a given volume of air contains only half as many molecules as the same volume at sea level. Although 21 per cent of these are oxygen molecules, as at sea level, it is obvious that the absolute amount of oxygen has been reduced by one-half. Under such conditions, and increasingly at higher altitudes, the metabolic requirements for oxygen exceed the available supply; exhaustion, and in extreme cases unconsciousness and death, results. In high-altitude mountaineering, and in some military aircraft, auxiliary supplies of oxygen are commonly used. In commercial aircraft designed for operation at high altitudes, the air in the cabin is artificially maintained at approximately sea-level pressure.

It has been demonstrated experimentally that many terrestrial invertebrates, such as insects, can survive for long periods under conditions of reduced barometric pressure equivalent to altitudes of as much as 15 miles above sea level. It is questionable whether in these experiments the upper limits of survival are imposed by oxygen lack, by desiccation, or by some more direct effect of reduced pressure itself. There are clear indications, however, that the absence of insects from high mountain ranges is not dictated by oxygen deficiency; the experiments demonstrate that insects are tolerant of more extreme oxygen deficiencies than any found naturally on the surface of the earth. The temperature conditions at high altitudes are probably the limiting factor in this case; temperature decreases with increasing altitude at an average rate of 6°C. for every 3280 feet, to a minimum of −55°C. near 36,000 feet.

Water and Salts. Water, containing many salts and other substances in solution, is the most abundant compound in the bodies of organisms. The ability of an animal to maintain a favorable water balance between its internal and external environments is of great significance in determining its survival. The interchange of water between the internal and external media involves its passage through living membranes, and such movements of water obey the physical laws of diffusion and osmosis. Therefore, in aquatic organisms, the maintenance of a proper water balance depends to a great extent on the relative concentrations of materials in solution in the body fluids and in the surrounding water; and the question of water as an environmental factor cannot be considered apart from that of the materials which the water holds in solution. We may think of a concentrated aqueous solution of salts as containing relatively less water than a more dilute solution. Hence, the ocean is a relatively drier environment than fresh water, and marine and fresh-water animals face very different problems in their water relations with the environment. Sea water is of rather constant composition, its salinity averaging about 35 parts per 1000. The body fluids of many marine animals, notably vertebrates, are much more watery than sea water, and adaptation to survival in a marine environment must involve perfection of mechanisms to imbibe water and eliminate salts, and to counteract the tendency of the body to lose water to the environment. Fresh waters vary widely in salinity; they are never free of salt, but in general animals inhabiting fresh water must be adjusted to a range of salt concentration far lower than that of their body fluids. The tendency here, which must be constantly counteracted, is for water to enter the body and dilute its fluids.

In addition to their effects on osmotic relations, the salts in the external medium are the source of specific ions necessary for the survival of aquatic organisms. The vital functions of organisms require that certain substances be available in minimum concentrations, to maintain the chemical constitution of the body fluids. Aside from its unfavorable osmotic effects, distilled water is unsuitable as a medium for aquatic life because it lacks the necessary materials in solution. Specific examples of individual requirements are furnished by crustaceans and mollusks, which are excluded from waters deficient in calcium carbonate; without this material the organisms are unable to secrete and maintain their exoskeletons.

Aquatic organisms are commonly adjusted to life within a specific range of salt concentration, and thus to particular ranges of water conditions. Adaptations of common occurrence involve modifications of the body wall to minimize general gain or loss of water, and special activities of the gills, excretory organs, and intestinal epithelium to conserve or eliminate water and salts. In simpler animals contractile vacuoles and protonephridial systems come into play. Usually the limitations of these adaptive mechanisms restrict the animal to either fresh or salt waters, but there are, of course, wide variations in the tolerances of different species to changes in the medium. These differences are most striking when we compare the adaptability of animals inhabiting tidal waters, such as the estuaries of rivers, with that of related marine and fresh-water forms in localities where they are not subjected to periodic tidal fluctuations in salinity. The broadly distributed estuarine species are tolerant of large variations in salt concentration. The essentially fresh-water forms at the upper end of the estuary are very often excluded from more brackish waters by increases in salinity of as little as one or two parts per thousand. At the other extreme, truly marine species are excluded by their inability to regulate their water balance in the face of periodic dilution of estuarine waters by fresh water from upstream.

The most striking and best-known examples of unusual adaptability are furnished by certain migratory forms, such as salmon and eels. For example, young salmon hatch in the headwaters of certain rivers, where the salt concentration is very low. As juveniles, they migrate to the ocean and then pass several years as marine fish. At maturity, they again enter the rivers of their origin and make their way to the headwaters for breeding. Eels exhibit essentially the reverse pattern, hatching in the sea, spending their maturing years in rivers, and returning to the ocean for breeding. The exceptional physiological adjustments involved in maintaining the water balance in the face of such extreme variations in external conditions must be far-reaching indeed.

For terrestrial organisms, the availability of water is of the utmost significance as an environmental factor. By definition, terrestrial animals are more or less independent of water as an environmental medium; nevertheless, the maintenance of a favorable water balance is no less important for these than for aquatic forms. There are great variations in the tolerance of different species to differences in the availability of water. At one extreme are such forms as the isopod crustaceans, earthworms, onychophores, and amphibians, which depend, at least in part, on a moist skin for respiration. These may be considered as only imperfectly adapted to terrestrial life; they require very moist environments, and as we have seen, most amphibia and some insects depend on water as an environmental medium for their developmental stages. At the other extreme are found the many species of insects, mammals, and reptiles, in particular, that are adapted to life under arid desert conditions. Between these extremes lie the great majority of terrestrial animals, with widely varying degrees of adaptation to abundance or scarcity of available moisture.

The water relations of terrestrial animals involve balancing gain against loss. Water may be obtained by drinking, by eating succulent food, by utilizing "water of metabolism" yielded in the metabolic breakdown of even dry foods, or by absorption from a moist environment. Water is lost chiefly by evaporation, through the skin generally or in the organs of respiratory exchange, or by its use as a vehicle for the elimination of egesta and excreta. Successful adaptation to dry conditions is correlated with extreme economy of water, with emphasis on prevention of evaporation, and on reclamation and reutilization of water involved in the process of excretion. Mammals, in which evaporation of water from the skin is an important aspect of temperature regulation, must make good this water loss by commensurate intake of water.

In terms of the availability of water, as with other environmental factors, each species of terrestrial animal exhibits a specific range of tolerance, beyond which it cannot survive. This is clearly illustrated by experiments with developmental stages of various insects which deposit their eggs on surfaces exposed to air. During the embryonic period within the eggshell, atmospheric humidity largely determines gain or loss of water by the insect through the shell and its membranes. Similar series of eggs, maintained at a constant temperature but under different conditions of atmospheric humidity, show very definitely the range of tolerable humidities, and in some cases a narrower zone of optimum humidity, for embryonic development. In some species development and hatching occur only in an atmosphere of 100 per cent relative humidity, saturated with water vapor. In other species, as illustrated by Figure 19.3, such a high humidity may be slightly less favorable than lower ones. The eggs of some species are so well protected against evaporation that development proceeds normally even in a perfectly dry atmosphere. In such conditions young larvae often die of desiccation as soon as they have ruptured the eggshell at hatching. Similarly, larvae may be unable to survive in saturated atmospheres after completing their embryonic development. In the experiment illustrated by Figure 19.3, more larvae developed than were able to survive after hatching, at all degrees of humidity, but particularly at

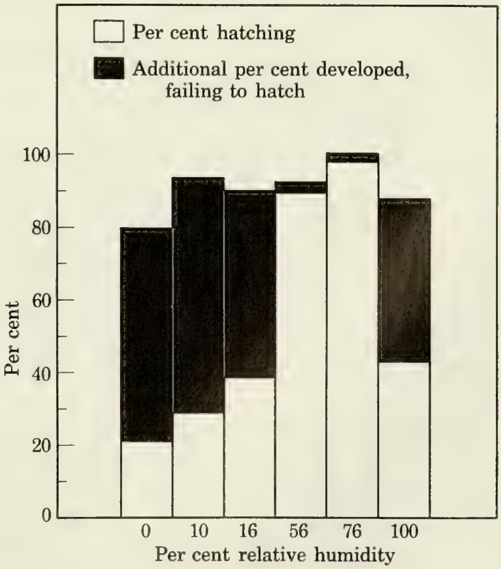


Fig. 19.3. Effects of different relative humidities, at a constant temperature, on the development and hatching of eggs of a moth, *Telea polyphemus*. (From D. Ludwig and J. M. Anderson, 1942, *Ecology*, vol. 23, reprinted by permission.)

those above and below the optimum. This illustrates the general principle that the water relations of a species may not be the same at different phases of the life cycle; humidities suitable for embryonic development may be too low or too high for larval survival. Projecting these experimental results into conditions in nature, we may conclude that a species of insect will occur only in environments where the humidity is within the limits of the range permitting development and survival of all stages, including the most susceptible, in its life cycle.

It should be borne in mind that, as pointed out earlier, there is a direct relationship between atmospheric humidity and temperature. Changes in temperature affect the drying power of air, as markedly as they determine the solubility of oxygen in water. In comparing the results of humidity experiments at different temperatures, it is often difficult to separate the direct effects of temperature from those of temperature acting through humidity.

General Considerations. We might analyze the limiting effects of a great many additional physical factors, such as acidity or alkalinity of the medium, light and other radiations, movements or currents in the medium, and so on. But the examples just discussed should suffice to demonstrate the general effectiveness of physical environmental factors. We may then proceed to draw several broad conclusions, with the understanding that they are supported by a great body of ecological data.

► For each species of animal, every physical factor in the environment imposes its own specific and peculiar limits to survival and distribution, and these limits may differ for different stages in the life cycle of the individual animal.

► A particular species can exist only in environments in which none of its tolerable limits of survival is exceeded, including those of its most susceptible stages.

► For any specific environmental factor, the limits of a given species may be close together (narrow range of tolerance), or they may be widely separated (broad tolerance).

► It follows that a species will be most stringently restricted in its distribution and survival by the single factor for which it has the narrowest range of tolerance; this is the factor of most significance in determining the existence of the species in any potential habitat.

► A species with no very narrow tolerances will be found almost universally distributed in the general type of habitat to which it is adapted, but even a related species with one or a few specific narrow tolerances will be less broadly distributed.

Animals are seldom found in habitats where one or more physical factors approach the limits for survival of the species. Exceptional are animals, incapable of migration, making a last stand for survival in an environment undergoing relatively rapid changes in a direction unfavorable to the species. More commonly, animals occur under conditions which approach the optimum. Here they function with greatest efficiency, reproducing and developing most rapidly, and expending the least energy in counteracting the effects of unfavorable environmental tendencies. In relation to physicochemical factors, the evident harmony between the animal and its environment results from **avoidance** by the animal of markedly unfavorable conditions, **acclimatization** of the individual to prevailing conditions within its limits of tolerance, and gradual **adaptation** of the species, by selection, through changes in its tolerances.

The Biotic Environment

Every environmental situation capable of supporting life, whether it be a sand dune, a fresh-water pond, a marine tide pool, or the intestine of a frog, contains a characteristic population of different kinds of organisms. All these organisms are adapted to the prevailing physical conditions of the habitat, and collectively they form what is termed a **community**. The fundamental character of the community is determined by the nature of the habitat, that is, by its physical features. Superimposed upon these are the biotic factors, which bind the members of the community together in a complex fabric of action and reaction. In a typical community careful investigation of the animals alone may reveal thousands of individuals, of dozens of species, representing several different phyla. Considering the plant species in addition (and even in animal ecology, the plants may not be ignored), the immense difficulty of establishing clearly the interrelationships within such a community is apparent. The complexity of typical communities, and the numbers of organisms involved, have indeed been obstacles to rapid progress in this aspect of ecology. Yet from the many excellent studies which have been made there emerge several principles, apparently of universal applicability to problems of the interrelationships between organisms within communities. We shall discuss some of these principles in the paragraphs that follow.

Food Relations. Only plants of various kinds, and the relatively few species of photosynthetic green protozoans, are capable of utilizing directly the radiant energy of sunlight. All other organisms depend on foods for their energy; that is, on the energy-rich organic compounds contained in the bodies of other organisms. Foods constitute the most important single requirement of animals, and it is not surprising to find that the basic relationship between organisms in a community involves their food requirements and food supplies. As indicated in Figure 19.4, the members of the community are interconnected by definite **food chains**, each animal feeding upon the kind next below it in the chain and itself serving as food for the type next above it. Thus, the fundamental relationships between animals are those of predator and prey. A particular kind of animal may have a place in more than one food chain, and hence the chains intermesh to involve the entire population of a community in what are sometimes termed **food webs**.

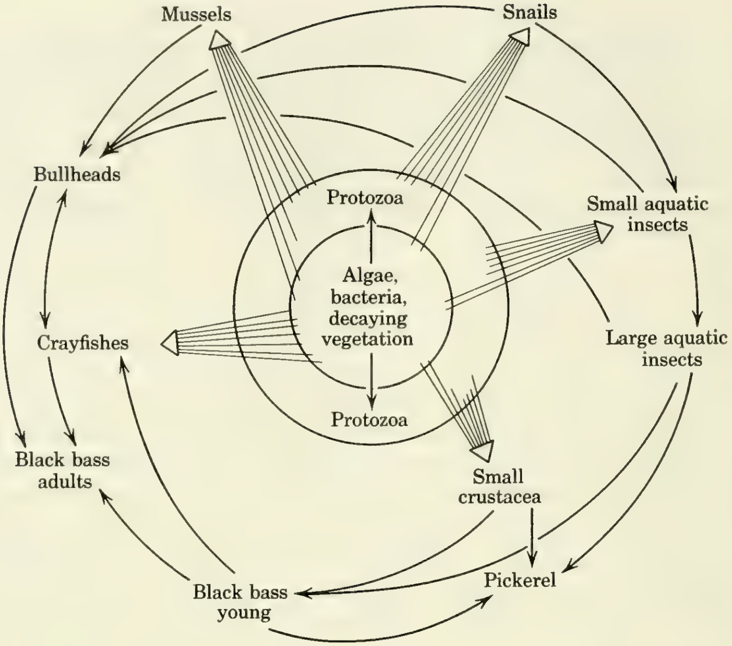

Mussels
Snails
Bullheads
Protozoa
Small aquatic insects
Algae, bacteria, decaying vegetation
Crayfishes
Large aquatic insects
Protozoa
Black bass adults
Small crustacea
Pickerel
Black bass young

Fig. 19.4. Schematic diagram of predator-prey relationships in a pond community. The arrows in each case lead from prey or food to predator or feeder; they may be interpreted as meaning "eaten by." (Adapted from V. E. Shelford, *Animal Communities in Temperate America*, copyright 1913 by Chicago Geographical Society, printed by permission.)

In analyzing one of the food chains in the pond community represented in Figure 19.4, we find that the microscopic green plants called algae serve as food for protozoans; these, and algae, are eaten by small aquatic insects, which in turn support a population of larger aquatic insects. The large insects are eaten by fish called bullheads, many of which are preyed upon by black bass. Adult black bass, if large enough, may be the terminal link in this chain, but smaller bass are important items in the diet of the larger pickerel. At almost any stage in this sequence, it is possible to follow alternate pathways, all of which, however, lead eventually to the pickerel.

Implicit in these intricate interrelationships are several interesting generalities. In the first place, plants form the broad base of the food relations of the community, because they alone are competent to entrap solar energy in the synthesis of organic compounds; plants, then, serve as the initial repositories of stored energy. In every community the plants support a population of **herbivorous** animals which transform plant materials into animal flesh. In our example, the protozoans, the small crustaceans, mussels, snails, and small insects represent the herbivorous links in the several food chains. These, in turn, serve as food for various **carnivorous** animals, which thus obtain stored solar energy very indirectly. In any food chain, there may be two or three, but seldom more, successive carnivorous links, until at last the chain terminates in a large carnivore which does not serve as prey for any other member of the community. These largest carnivores, while living, support only their indigenous populations of ecto- and endoparasites, although they may be preyed upon by transient carnivores, such as birds or bears, from other communities. If the pickerel die in the pond, their bodies are decayed by microorganisms, and their substance re-enters the food cycle as inorganic compounds required for the growth of aquatic plants.

Let us now consider **size of food** as it relates to the food chain. Note that in our example the successive links are: algae—protozoans—small insects—large insects—small fishes—large fishes. That is, there is a stepwise increase in the size of food from the beginning to the end of the chain. The large fishes do not feed on protozoans, or normally even on small insects; it is virtually impossible for them to capture enough of these tiny animals to satisfy their food requirements. On the other hand, neither do the small insects prey on the large fishes, which are beyond their ability to capture or ingest. Thus, every carnivore is restricted by its own limitations of size and strength to kinds of food small enough for it to manage; but there are also lower limits to the size of food which it can profitably handle. In short, the size of an animal largely determines its place in the complex predator-prey sequence called a food chain.

Related to the food chains, and also to the size of food, are certain considerations of **numbers of animals.** Every food chain represents what has been termed a "pyramid of numbers"; at every upward step in the chain, there is an increase in the size of organisms but a corresponding decrease in their numbers. In our pond, very large numbers of herbivores are required for the support of a smaller number of insects; these, in turn, suffice to maintain a few hundreds of small fishes, which furnish only enough food for a few dozen large fishes. In such an environment as that of the pond, limitations of space, sunlight, and available chemicals impose finite restrictions on the amount of plant growth that can occur. These restrictions are transmitted stepwise upward through the food chains, with the result that the maximum growth of plants will support, at the third or fourth remove, only a small number of the largest carnivores.

But why should this be so? The really significant factors underlying these numerical relationships appear to be considerations of mass and energy. As we have seen, the basis of food relations is the requirement of energy; but at every step in the food chain, about 80 to 90 per cent of the available energy is dissipated. For example, the flesh of the small fishes, upon which the large fishes prey, contains only about 10 to 20 per cent of the energy present in the bodies of the many insects supporting the small fishes. This accounts for the relatively small numbers of large carnivores in the community; in view of the inefficiency of energy transfer along the food chain, there is not enough energy left at the end of the chain to maintain more than a few terminal members.

This also offers an explanation for the fact that there are seldom more than two or three successive carnivorous links in a food chain.

The relationships just discussed in terms of the pond community exist, in a generally comparable way, in any natural community. In all, there are plants, herbivores, and varying numbers of carnivorous animals forming interlocking food chains. Among ecologists, each of these levels of activity is spoken of as a **niche**; and the niche occupied by a particular species in a community conveys an idea of its relationships with other members of the community. The types of animals occupying the various niches differ, of course, in different environments, but the parts they play are always comparable. For example, the very important niche of the chief herbivore in the community is filled in aquatic habitats by small crustaceans; in woodland and grassland communities, various small rodents, such as mice and rabbits, serve this function; in the arctic tundra, the principal herbivore is the lemming. In any community the maintenance of the whole superstructure of the food chains depends directly on the activities of the herbivores, and the activities of these animals are often referred to as the "key industries" of the various communities.

Exploring these relationships a bit farther, we find that in any environment there are usually a certain number of ecologically important niches to be filled. If through some catastrophe all the occupants of a particular niche in a community become extinct, the niche will eventually be occupied by some other type of animal. The new occupant may be an immigrant from another community, whose spread has been favored by the availability of the unoccupied niche. Alternatively, over a longer period of time, the vacant niche may be filled by the evolutionary appearance of a new form of life, adapted to the functions of the particular niche through natural selection from some ancestral type. In the fauna of oceanic islands, and of larger but similarly isolated land masses such as Australia, there are many examples of the formation of entire communities of animals through "adaptive radiation" from a generalized common ancestor. For instance, until the introduction of placental mammals into Australia and New Zealand, relatively late in historic time, all the mammalian occupants of various niches there were marsupials, with the minor exception of a few prototheres such as the platypus. The marsupials had evidently descended from a primitive, generalized ancestor of the opossum type, adapted in a bewildering variety of ways as herbivores and carnivores, with habits and requirements suited to the functional demands of the environment and the community (Fig. 19.5).

The complex interrelationships of the community are not necessarily invariable, however. There are many instances, as with ruminant mammals, in which herbivores are relatively large animals, and above these the food chain may consist of only a single carnivorous member. Also, many animals, by the development of special feeding adaptations or techniques, have found it possible to by-pass food chains. The whalebone whales, among the largest animals of the earth, feed almost exclusively upon microscopic crustaceans.

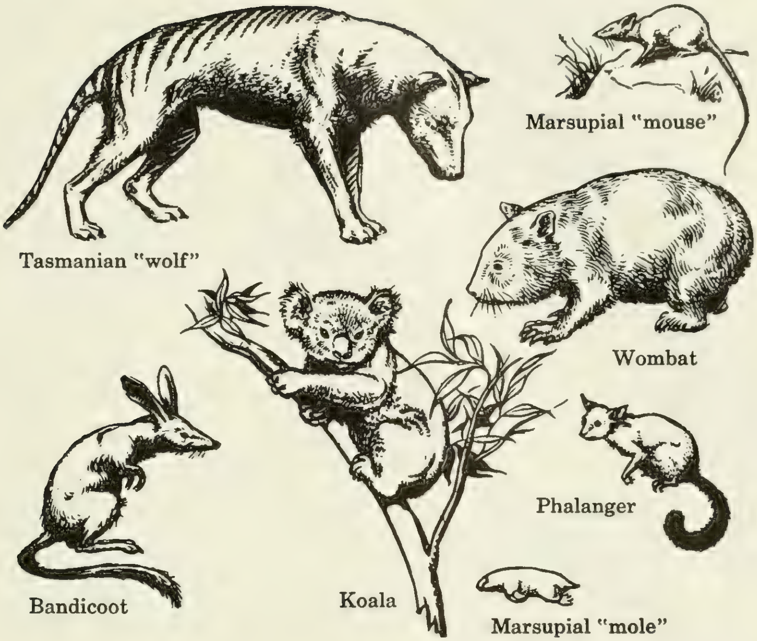


Fig. 19.5. Adaptive radiation among recent marsupial mammals of the Australian region. (From E. H. Colbert, *Evolution of the Vertebrates*, copyright 1955 by John Wiley and Sons, Inc., reprinted by permission.)

Having developed very efficient filters of "baleen," they are capable of ingesting the tiny herbivorous copepods in sufficient numbers to maintain life. Various carnivores are able, by hunting in packs, to exhaust and pull down large animals which would be beyond the abilities of the predators as individuals. Man, of course, by his inventiveness and ingenuity, obtains access to any desirable food, from the tiny seeds of grain crops to the flesh of the largest animals.

Animal Populations, Competition, and the "Balance of Nature." Theoretical considerations indicate that under ideal conditions the "innate capacity for increase" of a species, its reproductive potential, is unlimited. That is, populations are theoretically capable of increasing by geometrical progression from generation to generation. The numbers of animals which would be produced in even a few generations by such rates of increase are almost beyond belief. Elephants are relatively slow breeders, but a single pair of elephants would have at the end of 750 years nearly 19 million descendants, if all the individuals lived 90 years and each female gave birth to 6 young. More astronomical figures can be calculated for more rapidly breeding forms. An insect, the cabbage aphid, can produce 12 generations of offspring between the end of March and the middle of August. Each parthenogenetic female produces an average of 41 young. During a single

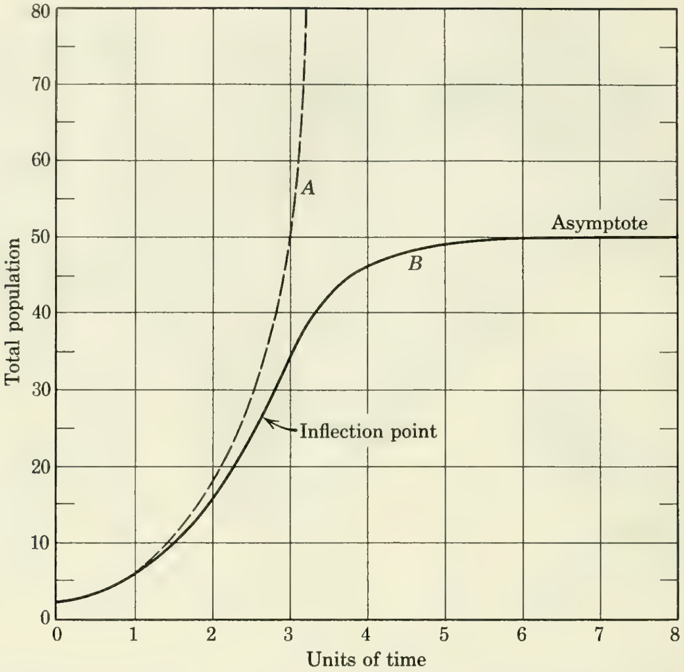


Fig. 19.6. Comparison of curves describing population growth. *A*, curve of geometrical progression, a theoretical possibility; *B*, logistic curve. (From G. L. Clarke, *Elements of Ecology*, copyright 1954 by John Wiley and Sons, Inc., reprinted by permission.)

breeding season, if all the offspring survived and reproduced at this rate, the progeny of a single female would number 564,087,257,509,154,652, and would weigh 1,645,254,501,068 pounds. From his studies on pedigreed cultures of *Paramecium*, Woodruff calculated that during a period of 5 years the number of descendants of a single individual, after 3029 generations, would be represented by 2 raised to the 3029th power. The volume of protoplasm in all these individuals would be not less than 10^{1000} times that of the earth.

Needless to say, the growth of populations of organisms under natural conditions is not described by a curve of geometric increase. Instead, it follows a sigmoid curve, often referred to as a **logistic curve.** The contrast between these two rates of increase, the ideal and the actual, is shown in Figure 19.6. In the logistic curve the rate of increase does not accelerate indefinitely; after a certain point, termed the **inflection point,** the rate of increase steadily diminishes, and the population thereafter approaches a maximum limit or **asymptote.** The events described by the logistic curve may be interpreted as follows. In the early stages of population growth, new individuals are added slowly, because the breeding stock is small. As the new individuals reach maturity and begin to add their own progeny to the population, the increase becomes more rapid; near the inflection point new individuals are being added at the maximum rate. But this rate of increase cannot be sustained, for now the population begins to approach the maximum number of individuals which the environment will support. Various environmental factors operate to increase the mortality rate; among these are (1) limitations of the food supply, (2) intensified predation and destruction by natural enemies, and (3) increased mortality from disease and parasitic infestation. Although the addition of new individuals (crudely, the "birth rate") may continue at a high level, the population does not grow larger indefinitely because of the concomitant increase in the mortality rate. Eventually, there is established an equilibrium between the "birth rate" and the "death rate," maintaining the population at levels which, averaged over long periods, approximate the maximum allowed by environmental conditions. We shall return later to consider the nature of this equilibrium.

The difference between the curve of geometric increase and the logistic curve represents the limiting action of environmental factors, the "checks against unlimited increase" which, as we shall see (p. 649), Charles Darwin embodied in his theory of evolution through natural selection. In addition to its tendency to increase in abundance, every species tends to increase its range and to spread more widely into new environments. Just as the environment sets limits on the abundance of a species within its range, so also environmental factors limit the distribution of animals. In a manner of speaking, checks against increase counteract the reproductive powers of the species, and its powers of dispersal are counteracted by other environmental factors. This control of distributional tendencies is another aspect of the equilibrium between animals and their environments.

In a natural community, then, populations of a species do not exist in isolation and do not find unlimited opportunity for increase and spread. Rather, they are involved in complex interactions with other organisms in the community, and an equilibrium is maintained among interacting species. It should not be supposed, however, that this equilibrium is a stable, unchanging balance between fixed numbers of organisms. For evidence of the dynamic, unstable nature of conditions temporarily in equilibrium, we may turn again to the fresh-water pond community analyzed in Figure 19.4, and quote Shelford, the originator of this figure:

> Any marked fluctuation of conditions is sufficient to disturb the balance of an animal community. Let us assume that because of some unfavorable conditions in a pond during their breeding period the black bass decreased markedly. The pickerel, which devour young bass, must feed more exclusively upon insects. The decreased number of bass would relieve the drain upon the crayfishes, which are eaten by bass; crayfishes would accordingly increase and prey more heavily upon the aquatic insects. This combined attack of pickerel and crayfishes would cause insects to decrease and the number of pickerel would fall away because of the decreased food supply. Meanwhile the bullheads, which are general feeders and which devour aquatic insects, might feed more extensively upon mollusks because of the decrease of the former, but would probably decrease also because of the

> falling off of their main article of food. We may thus reasonably assume that the black bass would recover its numbers because of the decrease of pickerel and bullheads, the enemies of its young. A further study of the diagram shows that a balance between the numbers of the various groups of the community would soon result. Under other circumstances, such as the extinction of the black bass, the resulting condition would be entirely different from the original one, but a balance between supply and demand would nevertheless finally be established.[1]

Thus, it is clear that any change in the environment, at any point in the food web, disturbs the existing dynamic equilibrium. The disturbance then, so to speak, echoes and re-echoes through the community, until a new, equally unstable equilibrium is established.

Shelford's statement also reveals something of the highly competitive nature of the relationship between different predators. Members of the same species, as well as different species of the same size and food habits, compete for a limited amount of food. Competition is not limited to food relations, however; individuals of the same species compete with each other for mates, and many diverse members of a community are in competition for space and for other requirements supplied by the environment. These competitive relationships should not be thought of as necessarily involving actual striving, or physical conflict; it is quite possible for two competitors never to encounter one another, if their habits are sufficiently different. The presence of one species may affect the environment in such a way as to make it unsuitable for another species, and very slight and indirect effects may be sufficient to tip the scales and lead to the extinction of a competitor.

With some knowledge of the approximate competitive relationships within a community, it is possible to predict the probable results of certain environmental changes, as Shelford has done in his analysis of the pond community. It is much more difficult to isolate two interacting species from a community for controlled experimentation, and to obtain quantitative data describing their interaction. This has been done, however, with two species of ciliate protozoans, with the results shown in Figure. 19.7. When *Didinium nasutum*, a predatory ciliate, is introduced into a sedimentless culture of *Paramecium caudatum*, the predator multiples until it has exhausted the supply of its food, *Paramecium*, after which the population of *Didinium* declines and dies out. When sediment is added to a similar culture, *Didinium* thrives for a short time and then disappears, whereupon *Paramecium*, some of which have escaped destruction by hiding in the sediment, is found to have survived the predator and to flourish with its extinction. To imitate another possibility in nature, periodic "immigrations" of *Didinium* can be arranged, with the result that the two populations show successive reciprocal peaks and declines. It is interesting, and has been substantiated by observations in natural communities, that the population peaks of predator and prey do not coincide; rather, as the numbers of predators increase, the intensity of predation also increases

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[1] From V. E. Shelford, *Animal Communities in Temperate America*, copyright 1913 by Geographic Society of Chicago. Reprinted by permission.

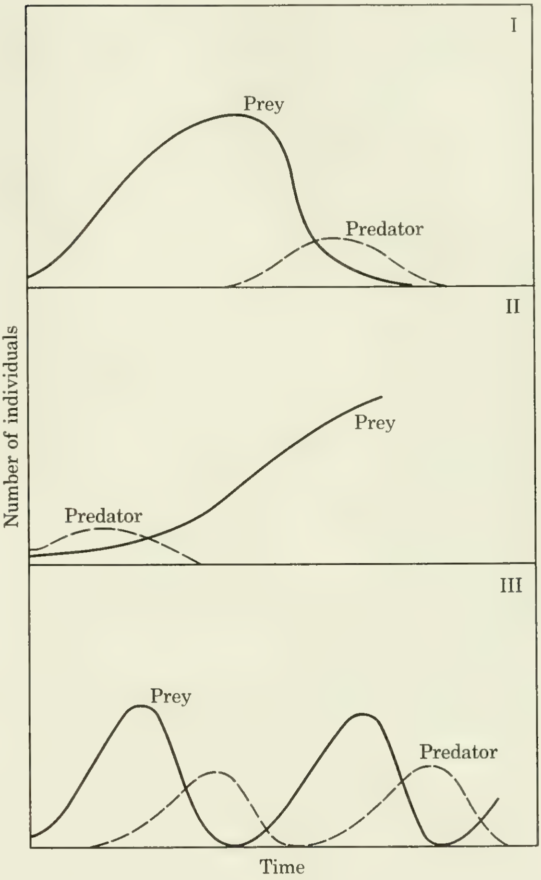


Fig. 19.7. Interactions between populations of *Didinium* (predator) and *Paramecium* (prey) under various experimental conditions. In a clean culture (I), the predator dies out after exhausting its food supply. Provided with sediment in which to take refuge, enough paramecia survive to flourish again after *Didinium* disappears, having destroyed all the prey it can capture (II). When the population of *Paramecium* is augmented by periodic "immigrations," (III), the two species may be maintained in a dynamic equilibrium of numbers. (Adapted from G. F. Gause, *The Struggle for Existence*, copyright 1934 by Williams and Wilkins, Inc. This modification of Gause's original figures is from W. C. Allee *et al.*, *Principles of Animal Ecology*, copyright 1949 by W. B. Saunders, Inc., reprinted by permission.)

and drives down the population of the prey species. Principles established by experimentation of this kind can be extended to the interpretation of predator-prey relationships, such as between two mammals, for which it would be impossible to set up exact experiments. An important feature of such experimental work is that the results are capable of mathematical expression, yielding data useful in the construction of mathematical models of conditions in natural communities. From such models it is possible to calculate and predict with some confidence the detailed effects of particular environmental changes.

The "balance of nature" is a phrase that has long been popularly used to describe the harmonious relationships between organisms and their environments. One important result of ecological studies has been to demonstrate that though there *is* a balance in nature, it is not a static equilibrium but one that even a slight change may disturb in unexpected ways. It is now possible to understand, for example, that the introduction of a few rabbits, or prickly-pear cactus plants, or Japanese beetles, or gipsy moths, into a "balanced" community is by no means such a minor event as it might seem. Relieved of the checks which restrain them in their normal environments, presented with abundant food supplies for which there is no strong competition, out of reach of their natural predators, they flourish unhindered, with far-reaching effects on the equilibria of established communities. Where man's livelihood and food supplies are affected, the economic cost of such importations is staggering. Under normal conditions the establishment of a new equilibrium, adjusted to the presence and activities of the immigrant species, is a very gradual process. However, through careful studies of the environments from which the immigrants came, it is often possible to discover parasites which operate there to keep them in check. Very often these parasites can be introduced into the invaded area, and through their activities the undesirable alien species may be brought under control. Rabbits have become a severe economic pest in Australia since they were introduced there; their numbers have increased in spite of hunting, trapping, fencing, and poisoning. Recently, their numbers have been much reduced by the introduction of a virus disease to which most of them are susceptible. It has been reported, however, that strains resistant to the disease have appeared, and it will not be surprising if breeding from these stocks repopulates the range with rabbits. The prickly-pear cactus was introduced into parts of Australia as an ornamental plant, but it spread so widely that millions of acres of grazing land in Queensland and New South Wales became covered with impenetrable thickets of the cactus. In 1925, several thousand eggs of the cactus moth, *Cactoblastis*, were collected in Argentina and sent to Australia to establish a colony of this species. The results of this introduction have been remarkable; the larvae of the moth feed upon the cactus plants, and, with the aid of a fungus which grows in their burrows, have destroyed the plants in a large part of their former range. Many other examples of the utility of such methods of "biological control" could be cited. These importations of controlling organisms must, of course, be conducted with the utmost care that the parasite does not, itself, have unexpected effects in a new environment on species other than its normal host.

Ecological Succession. Even the most stable environment, though equilibrium conditions prevail, is not constant or unchanging but undergoes continual fluctuations in both physicochemical and biotic characteristics. One aspect of successful adaptation to a habitat involves the ability to survive the customary periodic changes in any of its features. Environments may, however, undergo progressive alterations in a particular direction, as a result of which they become at length completely different environments. If these changes are sufficiently gradual, they may permit progressive adaptation on the part of the indigenous species, which thus survive with new adjustments. With more rapid environmental shifts, the limits of tolerance of the indigenous species are eventually exceeded in one or more respects, and these species, dying out or emigrating, cease to exist in the changed environment. Ordinarily, such consequences do not leave the habitat sterile, for other forms of life capable of survival under the changed conditions immigrate and flourish. During long-continued progressive changes the environment may harbor a series of many different communities, each composed of plants and animals adjusted to conditions of the moment, and each replaced by another as conditions continue to change. The orderly sequence of communities thus occurring is termed **ecological succession.**

Illustrations of ecological succession are common. For example, there is an annually recurring, seasonal succession in every temporary vernal pond. In the early spring such a pond is inhabited by communities of aquatic organisms requiring low temperatures; these are successively replaced by others as the water becomes warmer, and when it eventually evaporates in summer, there remains a damp or dry terrestrial habitat for exploitation by still other communities. Over shorter periods, succession may be studied in laboratory cultures of pond water. In these, we may observe the successive appearance, dominance, and decline of various kinds of protozoans, and of gastrotrichs, rotifers, copepods, and small annelids, as conditions change in the culture from day to day.

More striking examples of succession in nature occur on a larger scale and over longer periods of time. These may be set in motion by such events as the drying of rivers and lakes in prolonged droughts, the inexorable encroachment of sand dunes upon adjacent woodlands, and the filling of a pond with silt to produce a bog and, eventually, dry land. Studies of such events enable ecologists to chart the successive appearance and disappearance of specific plant and animal types, and to correlate each with prevailing conditions.

The most impressive changes, and those that should provoke thought in every citizen, are commonly the result of man's activities which alter the environment, usually as a negligent side result of some worthwhile project. Indiscriminately cutting or burning timberlands, cultivating or overgrazing dry prairie grasslands, polluting harbors and streams with oil, industrial waste, and sewage, man has destroyed ecological equilibrium conditions established through centuries of slow successions of communities. There is a growing public awareness of these problems; by analyzing and calling attention to the consequences of such practices, the ecologist makes a significant contribution to the conservation and proper utilization of natural resources.

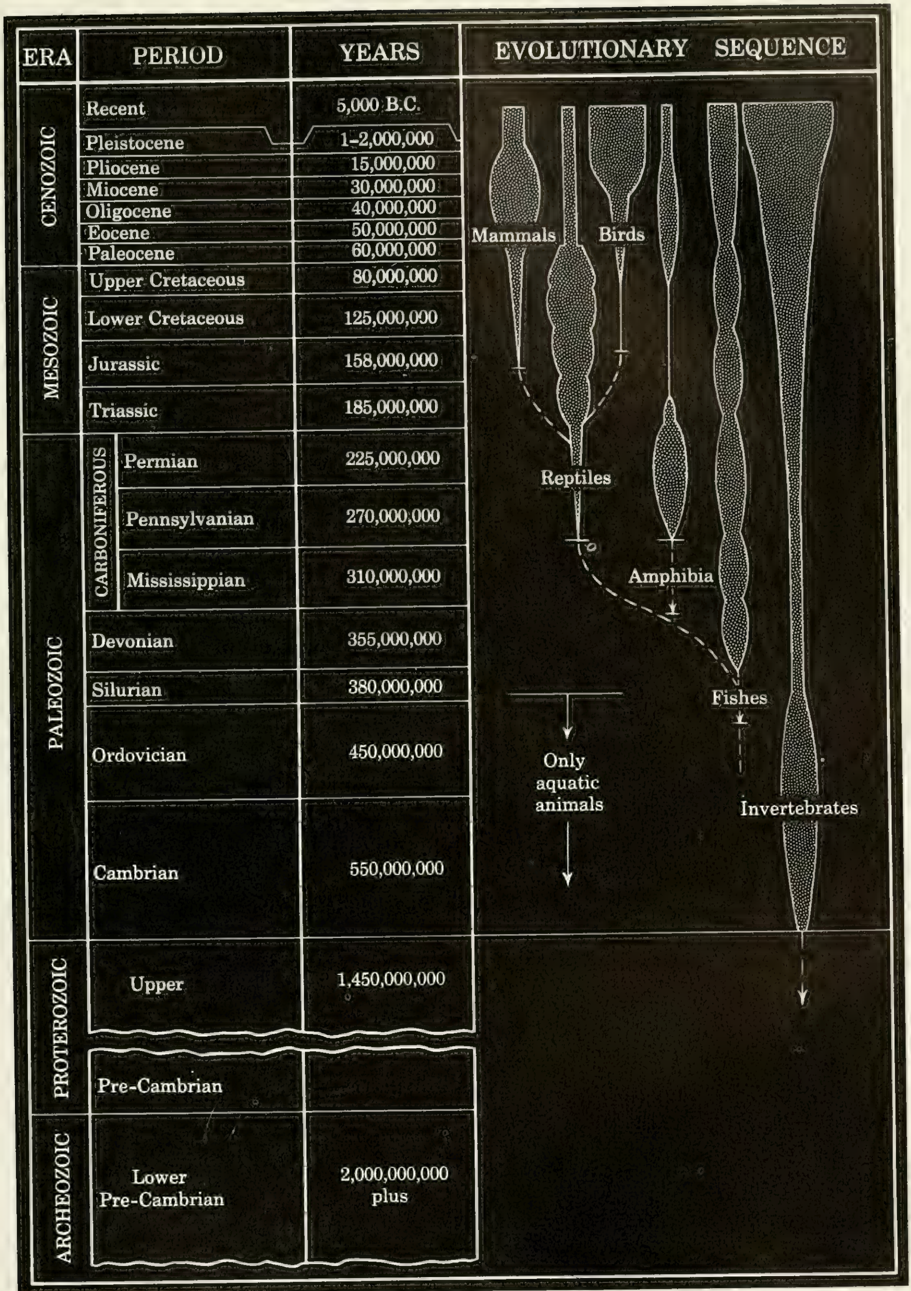
CHAPTER 20

THE EVOLUTION OF ANIMAL LIFE

MARINE BIOLOGICAL LABORATORY
WOODS HOLE

The term **evolution** connotes a gradual and continuous process of change, over long periods of time. This process of change is apparently a universal phenomenon; we know of nothing that is unchanged or unchanging. Compelling evidence from studies in astronomy indicates that the universe, together with that infinitesimal part of it which comprises our solar system, has undergone evolution on a cosmic scale through countless aeons. The study of geology presents equally strong evidence that the planet Earth has been subject to continuous evolutionary changes in its physicochemical features. In the course of this **inorganic evolution**, conditions consonant with life arose on earth; and at some subsequent time living systems appeared. Since their origin, these systems have undergone the gradual alterations in form and function which constitute **organic evolution**. Comparative studies of modern plants and animals, and of the fossil remains of their extinct ancestors, furnish abundant evidence of the reality of organic evolution. Although the fact of organic evolution is established to the satisfaction of scientists, the factors operating to cause or condition evolutionary processes are less easily understood. One of the most challenging problems of the present day—one which has intrigued several generations of biologists—is that of determining the mechanisms or processes through which organic evolution has come about.

In previous chapters the accounts of the various phyla of animals have been presented from the evolutionary point of view. The nature of existing animals, and the anatomical evidence of their phylogenetic interrelationships, can be reasonably accounted for only by assuming that organic evolution has occurred. In the present chapter we shall discuss the origin of life, consider the nature of the several lines of evidence supporting the concept of organic evolution, and present some of the theories that have been advanced to explain the available facts.



ERA	PERIOD		YEARS
CENOZOIC	Recent		5,000 B.C.
	Pleistocene		1-2,000,000
	Pliocene		15,000,000
	Miocene		30,000,000
	Oligocene		40,000,000
	Eocene		50,000,000
	Paleocene		60,000,000
MESOZOIC	Upper Cretaceous		80,000,000
	Lower Cretaceous		125,000,000
	Jurassic		158,000,000
	Triassic		185,000,000
PALEOZOIC	CARBONIFEROUS	Permian	225,000,000
		Pennsylvanian	270,000,000
		Mississippian	310,000,000
	Devonian		355,000,000
	Silurian		380,000,000
	Ordovician		450,000,000
	Cambrian		550,000,000
PROTEROZOIC	Upper		1,450,000,000
	Pre-Cambrian		
ARCHEOZOIC	Lower Pre-Cambrian		2,000,000,000 plus

Fig. 20.1. The geologic column. At the right are shown the approximate times of origin of the major groups of animals, and suggestions of the variations in their relative abundance during different periods. The figures given under Years refer in each case to the time elapsed since the beginning of the period. The Cenozoic periods Paleocene through Pliocene are sometimes referred to as the Tertiary, the Pleistocene and Recent periods together constituting the Quaternary. (Adapted from O. D. von Engeln and K. E. Caster, *Geology*, copyright 1952 by McGraw-Hill Book Co., Inc., printed by permission.)

The Origin of Life

It has been calculated that the earth was detached from the sun between 5 and 10 billion years ago. For a few billion years after its formation, the earth was presumably a glowing mass, far too hot to furnish an environment for any form of life. The historic record of the existence of organisms begins, in terms of our present knowledge, possibly as long ago as 3 billion years. Sedimentary rocks dating from this age contain spores of simple plant-like organisms. The level of organization of these fossilized traces of early life reveals, however, that they were the product of immense evolutionary advance during long antecedent periods of time. We must suppose that as the earth cooled and the watery hydrosphere condensed, living systems arose at least some hundreds of millions of years before the appearance of the organisms represented by our earliest fossils. There is no direct evidence about the nature of the environment on earth during these vast reaches of time. It may be speculated that in the primordial seas conditions of temperature, radiation, and chemical constitution favored the formation and persistence of an enormous number and variety of carbon compounds. Further, through random combinations among these substances, physicochemical systems of a relatively stable nature, with the fundamental characteristics of life, must have arisen. It has been suggested that these "proto-organisms" may at one stage have appeared in the form of "gene strings"—as aggregations of proteins and nucleic acids with the capacity of self-duplication, able to select materials from the surrounding medium and organize them into replicas of their own structure. As previously indicated (p. 262), we may interpret the existing viruses as modern representatives of this level of organization. It is possible that the viruses originated as free-living forms, in an environment which supplied all their requirements, although now they find only within the cells of other organisms the materials necessary for self-duplication.

It has been emphasized that at the present time living systems are not known to originate through any process of spontaneous generation. They occur only as organisms, and organisms arise only from pre-existing organisms. The fact that this is demonstrably true under present conditions does not eliminate the probability that living systems once arose, under very different conditions, from precursors that were non-living. We may simply reason as follows: life was not always present upon earth, and since life is now present, it must have originated at some time from non-living materials.

With the appearance of primordial living systems, the stage was set for the great drama of organic evolution. As the earthly environment continued to change, variant forms of organisms were always available with the capacity of survival under new conditions, and more conservative or less adaptable forms became extinct. The history of life on earth, from its inception to the present day, is an account of the evolutionary changes of living things. It is one of the most fascinating stories known to man.

Organic Evolution

According to the hypothesis just presented, the original living things did not appear as cells, but as much simpler aggregations of molecules possessing, as a consequence of their organization, the most rudimentary properties of life. A great epoch in organic evolution must have been marked by the gradual emergence of organisms in the form of cells, with division of labor between nucleus and cytosome. It may be supposed that this group of primitive cell-like organisms was ancestral to the existing protozoans and unicellular plants, all of which have evolved with great specialization as single-celled organisms. Another line of descent from the primordial unicellular forms attained the multicellular condition, perhaps beginning as persistent colonial aggregations of similar one-celled organisms. In this line the rise of true metazoan characteristics involved the differential specialization of individual cells for the performance of particular functions.

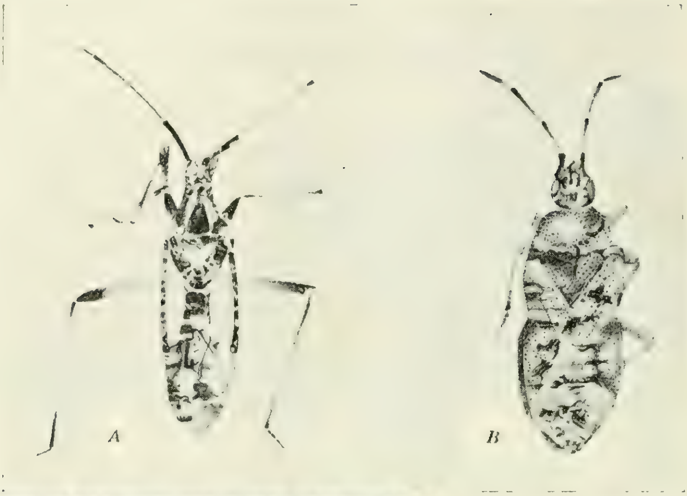
The facts of comparative anatomy and embryology suggest that the acquisition of such features as a gut cavity, some kind of body cavity, and bilateral symmetry were subsequent and successive steps in the evolution of the more complex types of metazoan animals. To postulate such broad steps in evolutionary change takes us, in time, far back of the earliest animal fossils; the evidence is suggestive, rather than conclusive. The phylogenetic tree presented in Figure 7.3, page 219, is based largely on such suggestive evidence. Within the more complex phyla, however, which have left a considerable fossil record, the evidence for later changes is much more concrete. Several specific examples of such well-documented sequences will be presented later in this chapter.

Evidence for the Fact of Evolution

We may now consider the evidence that has led biologists to conclude that the innumerable species of animals and plants now living, and all others that have lived in past times, have arisen through an evolutionary process. This evidence is subject to the same limitations as all historic data, but it has proved convincing because so many separate lines of evidence permit the same conclusions. Perhaps no single one of the principal lines would be considered sufficient in itself, but taken together, and reinforcing each other, they are very convincing.

EVIDENCE FROM DISTRIBUTION

Geologic distribution refers to the distribution in time of ancient forms of life, as revealed by paleontological studies of their fossil remains (Fig. 20.1). It may be contrasted with **geographic distribution**, which is the spatial or



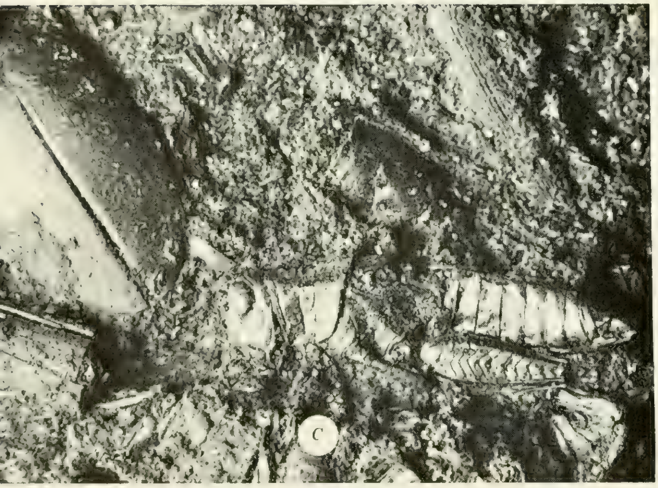


Fig. 20.2. Fossil insects. *A*, *Closterocoris elegans*, and *B*, *Lygaeus obsolescens;* these are fossil hemipterans found embedded in fine shales marking the bed of an ancient shallow lake, of Tertiary age, near Florissant, Colorado (*cf.* Fig. 15.29, p. 463). *C*, fossilized Pleistocene insects from the McKittrick tar bed, California; a locust and an aquatic beetle can be recognized. (*A* and *B* reproduced from the original lithograph plates in S. H. Scudder, 1890, *Report of the U.S. Geological Survey*, vol. 13; *C*, photograph by E. S. Ross.)

regional distribution of modern forms, the subject matter of zoogeography. Geologic distribution encompasses not only the temporal distribution of extinct organisms but also their geographic distribution in past times. Therefore, these two aspects of distribution cannot be entirely separated, any more logically than we can profitably study the anatomy of living animals without reference to the anatomy of animals known only as fossils. It is convenient to discuss the two aspects of distribution separately, however, before examining the correlations between them.

Geologic Distribution. Fossils and the fossil record have been referred to often in preceding chapters. Before we proceed to specific examples of the information to be gained from them, it is desirable to discuss briefly the nature of fossils and the manner of their formation. Fossils are the remains or traces of ancient animals and plants, usually preserved in the rocks. These rocks were themselves formed by the compaction and cementing together of deposits of silt, mud, sand, or volcanic ash, which had slowly settled out of the air, or out of streams, lakes, and shallow seas. Animals that died and fell into these deposits, or were overwhelmed by them, were buried by the accumulating sediments, often in large numbers. Their soft parts usually disappeared, through the normal processes of decay; but the shells or other skeletal elements of invertebrates, and the bones of vertebrates, were frequently preserved in some form or other. Very commonly, their original mineral constituents were leached out by ground water and gradually replaced by other minerals, to form hard and resistant petrifactions. Such fossils, differing in composition from the surrounding rock, are conspicuous when the rock is broken or eroded away. The shells of mollusks and brachiopods, and calcareous tubes of various annelids, often became filled with mud or silt upon the death and disintegration of the animal. Having turned to stone, this mud filling remains as an internal mold, after the shell itself has dissolved and disappeared. Similarly, external casts of the bodies of animals remain in sedimentary rock, although the bodies have disappeared from within them.

Delicate and soft-bodied organisms were rarely fossilized, for obvious reasons, but a few impressions of the bodies of large jellyfishes have been found in rocks of very fine structure. The bodies of aerial organisms, such as insects, were sometimes carried to the ground and buried by clouds of fine volcanic ash, or fell into bodies of water, to be entombed in sedimentary bottom deposits. The structure of the rock which these deposits subsequently formed is so fine that the delicate patterns of wing venation of the insects can be perfectly traced in their impressions. Some of the most valuable fossils of insects and other small terrestrial invertebrates have been found embedded in amber, which is the beautifully translucent substance formed by the transformation of gums exuded from ancient trees.

The skeletons of a wide variety of vertebrates and invertebrates have been recovered from peat bogs, and from tar pits such as the famous La Brea Pits near Los Angeles, California (Fig. 20.2). Through countless thousands of years, animals have become entrapped in these pits, and their skeletons have been infiltrated and preserved by the oily tar. Under entirely different circumstances, animals of the Glacial Period were sometimes frozen in ice and snow and their entire carcasses, complete with flesh and hide, preserved for extremely long periods, as were those of several mammoths found in Alaska and Siberia.

Traces of animals, as distinct from skeletons and impressions of their bodies, are of common occurrence in ancient sedimentary rocks. These traces include footprints of dinosaurs, found in great profusion in certain deposits in Texas and in the Connecticut Valley, as well as the tracks of worms and other invertebrates in rocks which represent the shores or bottoms of ancient seas (Fig. 20.3).

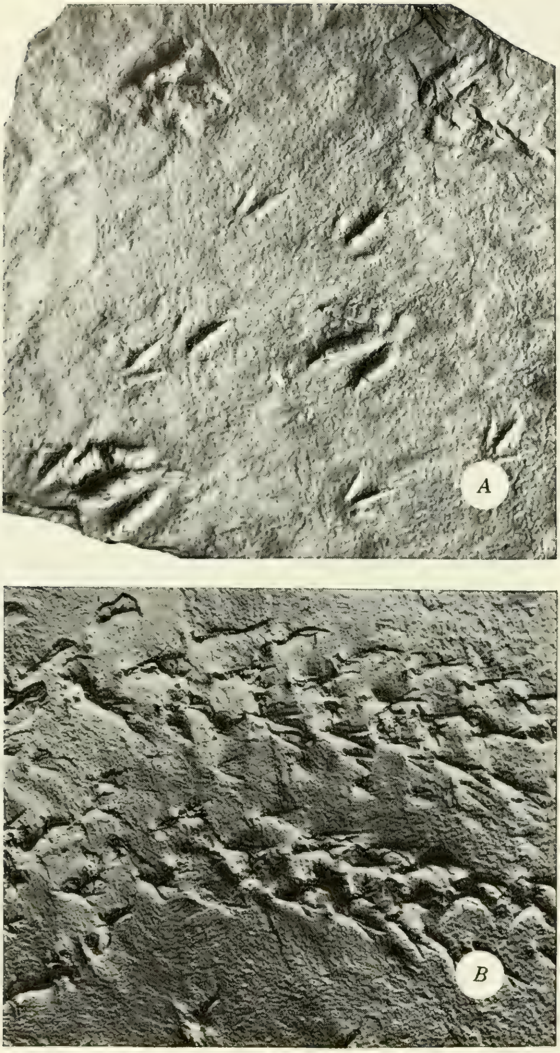


Fig. 20.3. Records of ancient life. *A*, footprints of large and small dinosaurs, from beds of Triassic age near Turner's Falls, Massachusetts; the large central print measures about 4 inches in length. *B*, *Limulus* trails, in rock representing a Devonian seashore. (*A*, photograph courtesy Peabody Museum, Yale University; *B*, photograph courtesy Dr. K. E. Caster.)

Thus, the remains of extinct animal life exist in a number of forms, but by far the most common, and the most valuable as records of the geologic succession, are the stony fossils embedded in the slowly accumulated sedimentary rocks. Even though the numbers of fossils seem enormous, it must be recognized that the fossil record is tantalizingly incomplete. Although many complete and perfectly preserved fossil skeletons have been found, the great majority of fossils are merely fragments of individual animals. When pieced together, they permit a fairly clear but far from perfect restoration of the animal as it was in life. In addition, since the chances were small that the remains of any individual organism would become fossilized, the known species represented by fossils include only a tiny fraction of the animals and plants that have inhabited the earth. All in all, however, the fossil record constitutes our best source of information about the forms of life existing in past times.

Aside from the information they yield about the characteristics of individual animals, fossil remains from sedimentary rocks make possible the establishment of an orderly chronology for extinct types of animals. In view of the manner in which sediments are deposited in water, it is obvious that the oldest layers, or strata, will be found at the bottom and the youngest at the top. This is true even though entire deposits have been elevated thousands of feet above sea level, subsequent to the time of their original formation. In many places this elevation has occurred without disturbance of the horizontal relationships of the strata, and it is possible to recognize not only the fossils but also traces of ancient topography, as when there are signs of beaches, mud flats, or deep waters. In other parts of the earth, particularly in great mountain ranges, strata that were originally horizontal have been folded during their elevation. The arrangement of the layers may be further complicated by the occurrence of breaks in the strata, known as faults, and by the horizontal slippage of one side of such a fault to overlie the other. By studying the rock outcrops in all parts of the world, with their included fossils, geologists have been able to piece together a series of sedimentary formations, the lowest resting upon earlier igneous rocks. This series constitutes the record of geologic history. The positions of the fossils in these strata indicate the order of appearance, or geologic succession, of the various forms of life. The relative ages of the different deposits are determined by their positions, and the absolute ages of the strata may be calculated, within certain limits of error, by special physical methods.

In the fossil record as thus set forth chronologically, there is a succession from simpler to more complex and more specialized types of animals (see Fig. 20.1). This sequence is of the greatest significance as evidence for organic evolution. Not only are the animals of the past different from those of the present, but the fossil record begins with forms that are vastly different. These are gradually succeeded by others that become more like modern forms, until they merge with those now living. There are many gaps, and many forms known as fossils have no close relatives among the modern fauna, but the geologic succession shows the grand course of evolution so far as it can be ascertained from the fossil record.

Special Examples of Geologic Succession. ***Invertebrates.*** There are many instances among invertebrate groups, particularly in mollusks and brachiopods, where the succession of fossil remains is comprehensive enough to show in some detail the various courses taken in evolution. A good example is furnished by the ammonoids, a large group of cephalopod mollusks which flourished in Paleozoic times (see p. 388) but are now extinct (Fig. 20.4). The ammonoids can be traced to a common ancestry with the nautiloids, another cephalopod group from which they diverged during the Silurian.

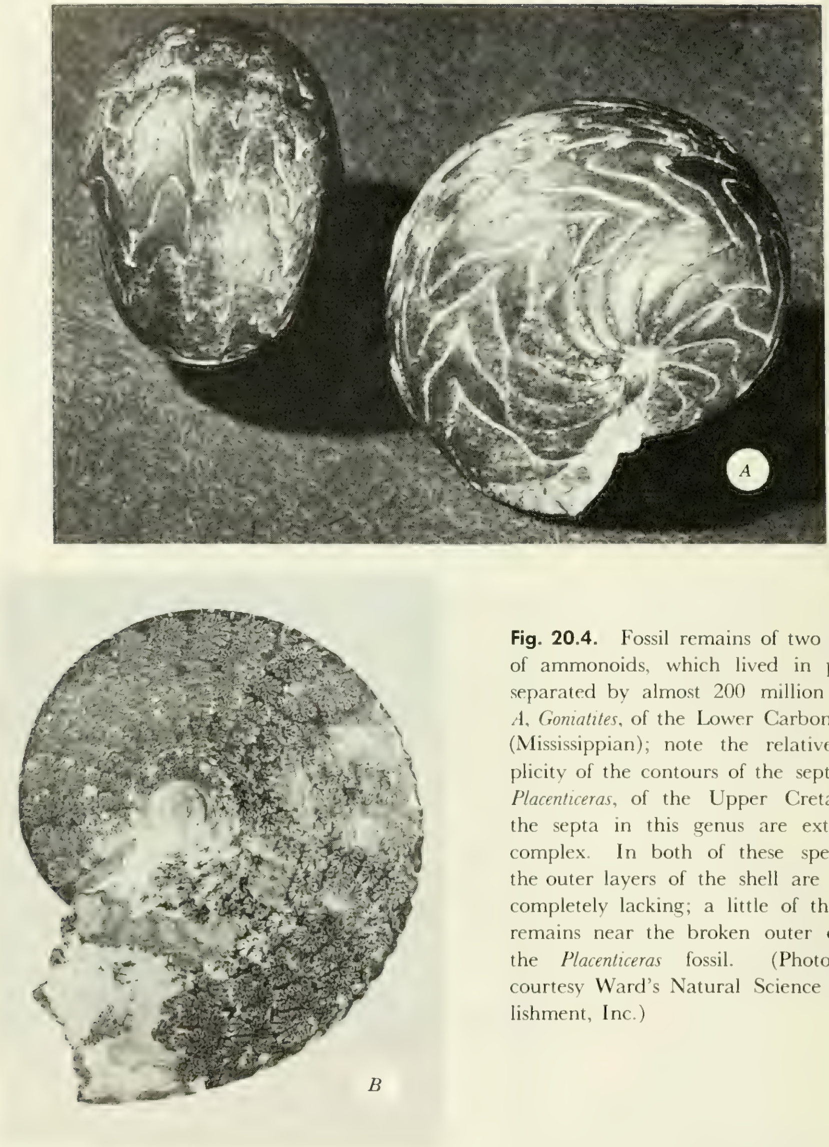


Fig. 20.4. Fossil remains of two genera of ammonoids, which lived in periods separated by almost 200 million years. *A*, *Goniatites*, of the Lower Carboniferous (Mississippian); note the relative simplicity of the contours of the septa. *B*, *Placenticeras*, of the Upper Cretaceous; the septa in this genus are extremely complex. In both of these specimens the outer layers of the shell are almost completely lacking; a little of the shell remains near the broken outer end of the *Placenticeras* fossil. (Photographs courtesy Ward's Natural Science Establishment, Inc.)

Ammonoids are known only from their fossilized shells, or exoskeletons; these demonstrate a long succession of forms culminating in large and highly elaborate shells. Ammonoids occurred in such numbers and in such a wealth of species that during the Jurassic and Cretaceous they were probably the dominant forms of marine invertebrate life. Later, at the close of the Cretaceous, this entire subclass of cephalopod mollusks became extinct; there are none in the modern fauna, and no fossils of ammonoids are known subsequent to the Cretaceous. Remnants of another line of descent from the ancient ancestral stock persist to the present, however, represented by the genus *Nautilus*, which is now limited to the tropical Pacific and Indian Oceans (see Fig. 13.16, p. 388). Thus, *Nautilus* has preserved the general organization of its remote ancestors, without substantial change, through a span of time vastly longer than that required for the evolution of the entire series of vertebrate animals. This is an exceptional case; the great majority of animals have become strongly modified during the passing ages, or, like the ammonoids, have become extinct.

Vertebrates: The Horse Family. The fossil record of horses is probably more nearly complete than that of any other mammalian type. The largest series of remains appears in fossil beds of the western United States, where horses flourished for a long period before they became extinct during the Pleistocene. In more recent times the members of the horse family (which includes horses, wild asses, onagers, and zebras) have been found in their original wild state only in Europe, Asia, and Africa. The "wild" horses of the Americas in recent centuries were the descendants of horses introduced by early settlers. The earliest native American horses, such as *Hyracotherium* (=*Eohippus*), the dawn horse (Fig. 20.5), are believed to have originated in some other region and migrated to North America; they appear in the fossil record here without recognizable antecedent types. Central Asia is suspected as the place of origin, although the ancestors of *Hyracotherium* have not yet been discovered there. The fossil record shows that the horse family flourished in North America for many millions of years; some of its members eventually migrated to South America and became widely distributed there. This southern branch of the family became extinct in the Pleistocene, along with the North American horses. The causes of this extinction, as those of the disappearance of ammonoids, dinosaurs, and many other types of animals, remain matters of speculation. One possibility is that all the horses of the New World may have been swept away by some epidemic. We know only that they disappeared in the New World, although a few species survived on the continents of the Old World; these Old World lines were apparently established by migrants from North America.

The fossil record gives a clear indication of the probable course of evolution, through which forms like *Hyracotherium* gradually evolved into horses of the modern genus *Equus* (Fig. 20.6). The series begins with small animals, ranging from the size of a small dog to half the size of a modern pony, with relatively short neck and limbs. There were four functional digits on each fore foot, three on each hind foot, with "splint bones" representing the vestiges of other toes no longer functioning to bear the weight of the body. The foot was also supported behind by a cushion-like pad. The characteristics of the feet and the teeth indicate that *Hyracotherium* was a forest-dwelling animal which browsed the leaves of bushy plants and low trees; the vestigial digits reveal that it had evolved from ancestors having five toes on each foot. The dawn horse was markedly different in many respects from modern horses—so

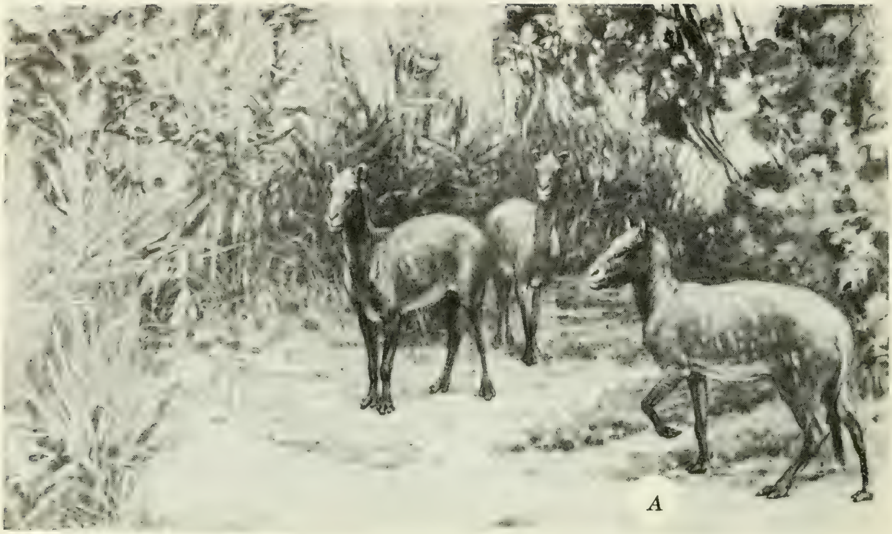
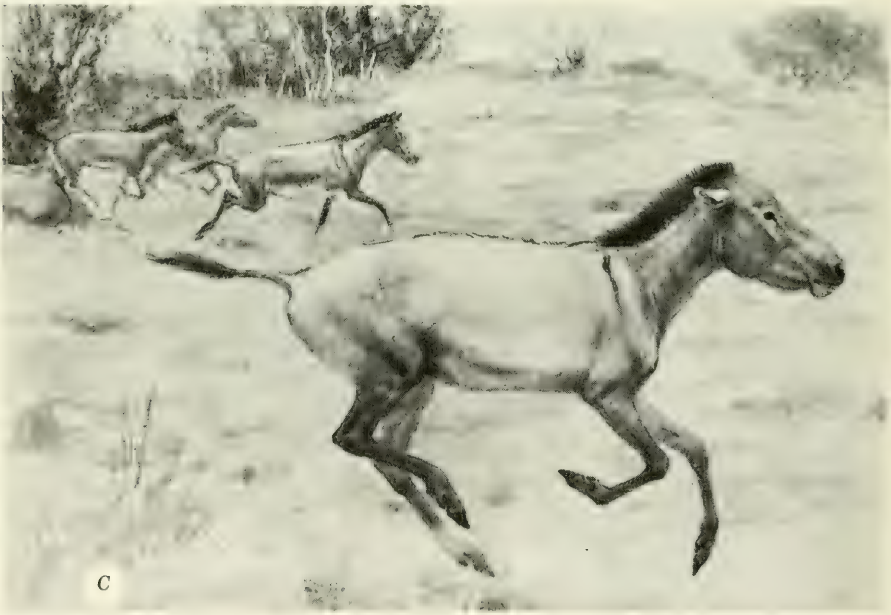
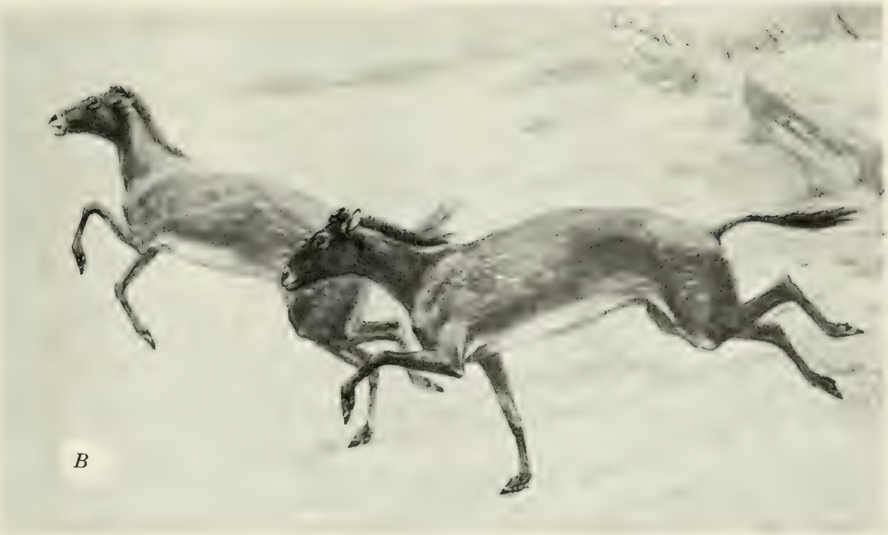


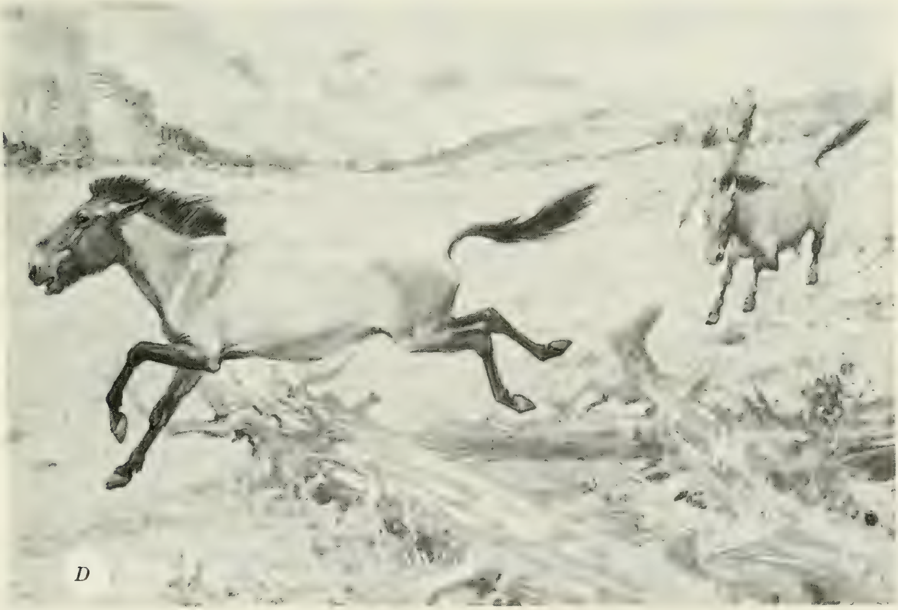
Fig. 20.5. Reconstruction of selected genera representing significant stages in the evolution of the horse family. *A*, *Hyracotherium* (= *Eohippus*), Eocene. *B*, *Mesohippus*, Oligocene. *C*, *Hipparion*, Pliocene; this genus is not on the main line of evolution of modern horses.



different, in fact, that without the fossil remains of numerous connecting forms they probably would not be considered related at all. The evolution of horses involved many independent lines, each culminating in different end forms at different periods. The evolutionary sequence leading most directly



D, *Equus scotti*, Pleistocene, an extinct species of the genus to which modern horses belong. The probable interrelationships of these and other genera are shown in the table, Figure 20.6. (Courtesy American Museum of Natural History.)



to modern horses was marked by a few general trends. These are correlated with adaptations for greater speed in running and with the change in environment from forest to grassy plains. The trends may be summarized as follows: (1) loss of side toes until only one functional digit remains in each foot,

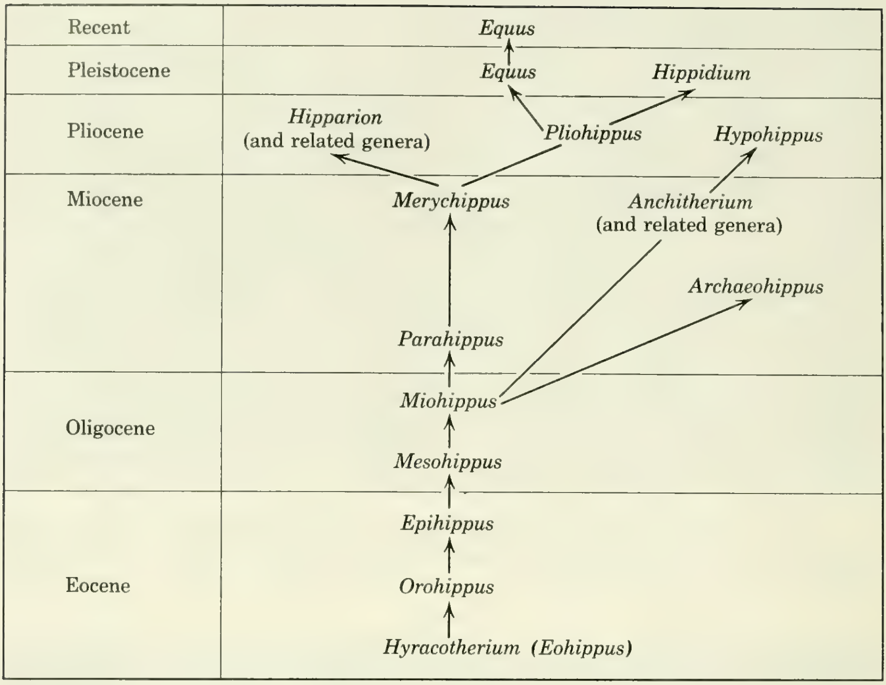

Recent
Equus
Pleistocene
Equus
Hippidium
Pliocene
Hipparion (and related genera)
Pliohippus
Hypohippus
Miocene
Merychippus
Anchitherium (and related genera)
Archaeohippus
Parahippus
Oligocene
Miohippus
Mesohippus
Eocene
Epihippus
Orohippus
Hyracotherium (Eohippus)

Fig. 20.6. Summary of the main lines of evolution of horses in relation to the geologic time scale. The general characteristics of some of these genera are described in the text, and reconstructions of some are shown in the preceding figure. (From E. H. Colbert, *Evolution of the Vertebrates*, copyright 1955 by John Wiley and Sons, Inc., reprinted by permission.)

and loss of the supporting pad with the development of specialized ligaments connecting the toe bones; (2) increase in length of the distal parts of the limbs, with fusion of the radius and ulna and of the tibia and fibula; (3) increase in complexity of the teeth, with differentiation for grazing and for grinding; and (4) increase in the size of the body and in the relative size of the brain. In none of these trends has there been a steady progression toward modern conditions; but these are the chief points of contrast when modern *Equus* is compared with its remote ancestors.

The Elephant Family. Another example of a relatively complete series of fossils demonstrates the succession of types apparently ancestral to modern elephants (Fig. 20.7). The oldest recognizable representative of the elephant family is *Moeritherium*, known from fossils in late Eocene deposits in what is now the Libyan Desert of Africa. Descendants of this form can be traced to all the other continents except Australia. *Moeritherium* had no proboscis (trunk) and no well-developed tusks; it apparently used its prominent front teeth for grubbing roots, more or less as swine do. As in the history of horses, the descent of elephants involved many separate lines,

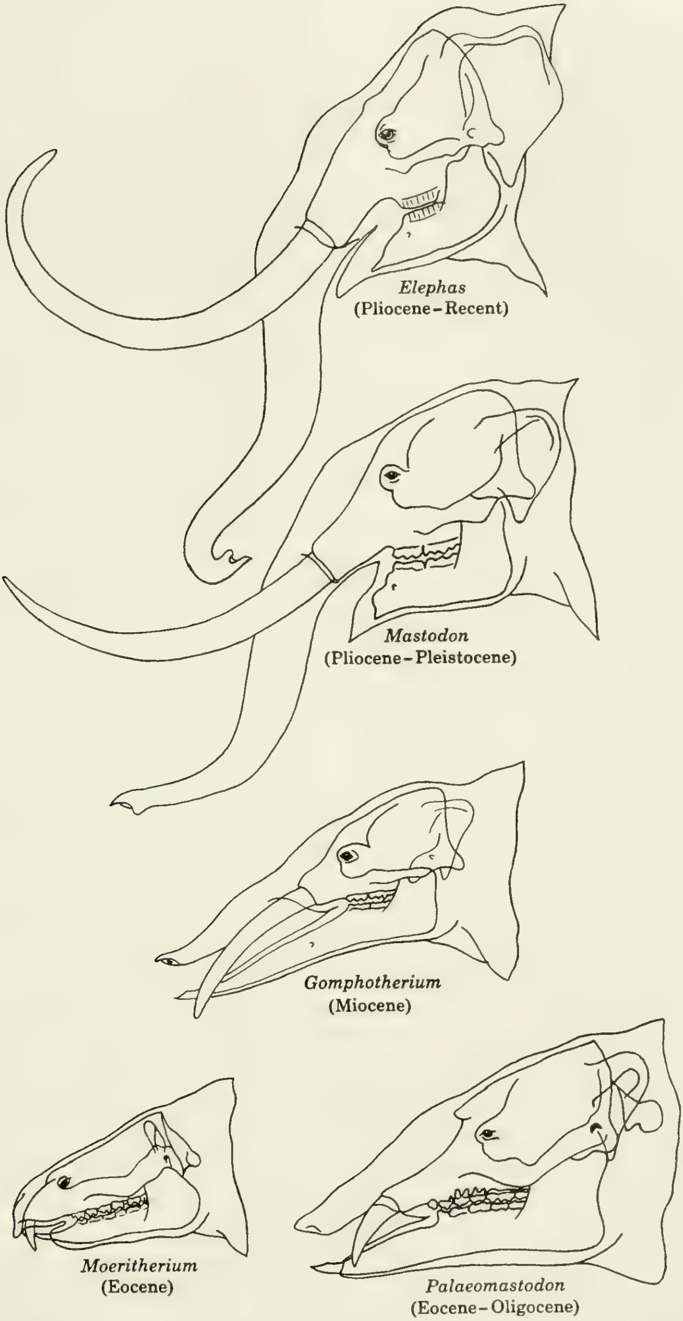

Elephas
(Pliocene–Recent)
Mastodon
(Pliocene–Pleistocene)
Gomphotherium
(Miocene)
Moeritherium
(Eocene)
Palaeomastodon
(Eocene–Oligocene)

Fig. 20.7. Representative stages of evolution in the elephant family, as shown by the skulls of selected genera. For proper comparisons of size, note that the lower two figures have been reduced twice as much as the upper three. The significant changes in the proportions of the facial parts involve an initial lengthening of the chin, followed by a marked shortening. These changes are correlated with the development of the proboscis, or trunk, and of the tusks. (Redrawn from R. S. Lull, 1908, *American Journal of Science*, Series 4, vol. 25, printed by permission.)

each with its own direction. In the sequence leading to modern elephants, however, the following changes are notable: (1) the snout becomes elongated to form the trunk; (2) the jaws become shortened; (3) the teeth become modified and complicated and undergo marked specialization, both in structure and in the manner of their succession; (4) the shape of the skull changes remarkably; and (5) there is a great increase in the size of the body and of the brain. Members of the elephant family flourished and ranged widely in Europe and North America but disappeared from both continents at the close of the Pleistocene. The mastodons, the only type which reached South America, persisted until recent times but eventually disappeared. Today, the only survivors of the elephant family are the modern African elephants and those native to Southeast Asia.

Synthetic Types. Critics of the general idea of organic evolution often raise the objection that the connecting links which should exist between various types of animals are not to be found in the modern fauna. It should be clear, however, that such links, or synthetic types, are not to be sought among existing animals but among fossils. The connecting links between different types of modern animals were their common ancestors, which have disappeared through extinction. The connections between modern horses, zebras, and wild asses were the extinct members of the horse family ancestral to all the modern types. The links between the Asiatic and African elephants, and between the existing south American guanacos and the camels of the Old World, were likewise the extinct common ancestors. The links between men and apes were the extinct prehuman primates, the earliest of which were more ape-like than man-like.

Connections between larger groups are not wanting; they are clearly represented by the fossil remains of forms transitional between amphibians and reptiles, between reptiles and birds, and between reptiles and mammals, as described in Chapter 18. It should not be expected that in these instances one single animal will show all the transitional structures. Striking examples of such transitional forms are the primitive birds, notably *Archaeopteryx*, which show many reptilian characteristics (see Fig. 18.25, p. 575). The development of a bird resembles that of a reptile, and the structure of the adults is more similar than would be supposed from casual examination. *Archaeopteryx* is perhaps as nearly a synthetic type as we could hope to find, in view of the imperfections of the fossil record.

In addition to the fossil remains of such forms, animals that are sometimes called "living fossils" still exist. The duckbill, *Ornithorhynchus* (see Fig. 18.30, p. 581), is an egg-laying mammal which may be regarded as a survivor not far removed, in its structural and reproductive features, from the egg-laying reptilian stock that gave rise to the mammals. The existing lungfishes may similarly be interpreted as links between aquatic and terrestrial vertebrates; these might have become extinct, like *Archaeopteryx*, but instead they have survived and lend support to the theory of evolution. The lobe-finned fishes (see p. 557) were believed to have been long extinct and were known only from their fossil remains until a living representative of one of the lobe fin groups, the Coelacanths, was taken from the ocean off South Africa in the late 1930's; since World War II, several additional specimens have been caught and are being intensively studied. Even entire groups, such as the sharks or the amphibians, may be regarded as survivals of ancient types that have descended with modifications but without changes in certain primitive features.

Geographic Distribution. Consideration of the geographic distribution of animals and its bearing on the problem of evolution requires that two fundamental concepts be borne in mind. First, the ancestors of related genera, for example, originate in a single locality, known as the **common center** of origin. Second, **migration** from this center occurs, for reasons previously discussed (see pp. 610 611). Geographic **barriers**, such as mountain ranges, large bodies of water, and the like, determine the direction of migration by interposing conditions which the animals cannot overcome or tolerate. Migration from common centers of origin, as directed by physical barriers, is believed to account for the observed distribution of animals on the surface of the earth. The natural distribution of animal types, occurring through countless centuries, has been increasingly disturbed by human migrations and the attendant transportation of animals and plants to new habitats.

As pointed out earlier, the problems of paleontology, which involve vertical or temporal distribution, are inseparable from those of zoogeography, which involve spatial or horizontal distribution. The present distribution of animals can be understood only in relation to the distribution of their ancestors during preceding millennia. This interrelationship is well illustrated by the camel family. As it is now distributed, this family consists of two widely separated groups. The genus *Camelus* includes two species, the Arabian camel, or dromedary, and the Bactrian camel of Central Asia. On almost the opposite side of the world, in the Andes of South America, occur the only other camel-like animals now in existence. These are species of the genus *Auchenia*, the guanaco and the vicuña, with their domesticated descendants, the llama and the alpaca. The surprising separation of these two groups of related modern forms can be logically explained only by the geologic distribution of the ancestral stock of camel-like animals. As shown by the fossil record, camels originated in North America as a family of hoofed mammals. Here they flourished from the Eocene to the close of the Pliocene epoch. Migrations occurred during the Pliocene, one group reaching South America, the other attaining Asia by way of a former land connection in the region of the Bering Sea. The extinction of the North American camels during the Pleistocene left representatives in South America and Asia, and it is from these widely scattered ancestors that the modern species have descended. Numerous other examples might be cited from the fossil record, all showing that the theory of organic evolution gives meaning to the present geographic distribution of many types of existing animals.

It is frequently possible to explain the peculiarities of an entire fauna, the animal population of a particular locality, by the extension of a similar line of reasoning. Geologically speaking, there are two types of marine islands: continental islands, such as Long Island and the British Isles, and oceanic islands, such as the Azores, Bermuda, and Hawaii. Continental islands are near continents, to which they were probably attached in past times; oceanic islands have appeared in the ocean without previous connection with any continent, or they may be the surviving mountain tops of former land masses. The faunas of these two types of islands bear out the theories of the geologic origins of the islands, and of the origins of the faunas by evolutionary processes. The native fauna of the British Isles resembles that of Northwestern Europe, with which they were evidently formerly connected. The native fauna of Hawaii, in contrast, is an odd mixture of forms and is unlike that of any continent. Presumably, as discussed in Chapter 19, the faunas of such oceanic islands have developed by adaptive radiation from chance immigrants which reached the islands on floating objects or otherwise. One of the peculiarities of Hawaii is that there are no native amphibians; these animals cannot tolerate exposure to salt water and have therefore been unable to reach the isolated islands. The continent of Australia has a fauna very different from that of Asia, because the two have been so long separated (see Fig. 19.5, p. 609). Eurasia, Africa, and North America have similar mammalian faunas because of former migration routes across land bridges from Alaska and by way of Greenland.

EVIDENCE FROM MORPHOLOGY

Comparative Anatomy of Adults. Whether we examine the broader features of anatomy in the several phyla of animals or the structure typical of a single group, such as vertebrates, we find everywhere facts that are most logically interpreted from the standpoint of evolution. In the vertebrates, two pairs of limbs, a trunk, head, tail, and various internal organs are always laid down according to a similar general plan, but with special modifications in relation to the mode of life. Therefore, it is possible to construct a plan which is characteristic of vertebrates in general. Similarly, as indicated in preceding chapters, a characteristic plan can be made for animals in each of the phyla; there is a coelenterate plan, an annelid plan, an arthropod plan, and so on. More specific resemblances in the corresponding parts of the body are revealed when comparisons are made among animals of a single class. Despite their differences, the flipper of a whale, the wing of a bat, bird, or pterosaur, the fore limb of a horse, and the arm of a man all show the same general plan of structure. Such similarities in fundamental design, despite special adaptive modifications for specific functions, illustrate the principle of homology; examples are numerous in every phylum of the Animal Kingdom.

Vestigial structures are of interest in the study of homology. These are structures which correspond in plan and in position to functional parts of related animals, but which are much reduced in structure and may be apparently functionless. Examples include the splint bones in the limbs of modern horses, the vestigial second and fourth digits; the tiny remnants of the hind limbs in pythons, representing structures which have entirely disappeared in most snakes; and the vestigial hind limbs of whales and other aquatic mammals. Vestigial structures are numerous among the more highly specialized members of any phylum.

We are thus faced with the problem of accounting for these facts of anatomy, in terms of the history of animal life. In pre-evolutionary interpretations, each species of animal, though created separately, was thought to have been formed in accordance with an ideal type, which explained the existence of homologous structures. This was the belief of Louis Agassiz (1807–1873), who, although a naturalist of great ability, was never able to adjust his thinking to the concept of evolution as set forth by Darwin in 1859. The idea of special creation after ideal forms is, of course, a theoretical possibility; to substantiate it, there should be objective evidence that animals originated in their present form and have never changed. As we have concluded from our survey of the fossil record, however, animals evidently did not originate in their present form but have changed remarkably during geologic time. The evolutionary explanation of the anatomical resemblances between animals states that all the members of a group, such as the vertebrates, have inherited a similar plan of organization from the common ancestors of all vertebrates. Each subdivision and species has been modified in particular ways in relation to its way of life; but all remain fundamentally similar, because they have never lost the underlying body plan that characterized their ancestors. Because whales and all other mammals had a common ancestry at a remote period, their fore limbs and many other parts retain certain similarities at present. Mammals resemble other vertebrates for similar reasons. Vestigial structures remain because they are a part of a persistent plan and have not been entirely lost, although they may be no longer functional. The comparative anatomy of adult organisms furnishes very telling arguments for the occurrence of organic evolution.

Comparative Embryology. Almost everyone who is at all familiar with the evidence for organic evolution has heard the statement that the individual in its development repeats the developmental history of the race. This general idea often takes the form of the aphorism, "Ontogeny recapitulates phylogeny." There is probably no statement in the whole field of biology that is more widely misunderstood. The **Recapitulation Theory,** as it has been called, maintains that certain developmental stages or structures are related to ancestral conditions; it is recognized that others may be adaptations to the present manner of development.

To cite a familiar example, the embryo of a fish develops gill slits, gills with specific blood supply, and a two-chambered heart; all these features persist in the adult fish. The development of a frog tadpole includes the formation of a similar organization, fish-like in the arrangement of gills and blood vessels and in the two-chambered condition of the heart. But these structures are completely reorganized during later development, which culminates in the metamorphosis of the tadpole into an air-breathing adult with lungs and a three-chambered heart. Embryonic development in reptiles, birds, and mammals produces rudimentary gill slits and a fish-like circulatory system, which are reconstructed in later stages to form a different adult organization. These stages in the development of vertebrate embryos are as well known as the facts of adult anatomy and can be observed by any student of embryology.

It is not surprising that the embryos of fishes, and even of amphibians, should develop gill slits, gills, and associated blood vessels; these forms develop in water, and the structures can be related to definite functions. But why do gill slits develop in reptiles, birds, and mammals, which are terrestrial organisms? Viewed in the light of an evolutionary interpretation, these developmental peculiarities are understandable. If the ancestors of vertebrates were originally fish-like animals, and if, as we have supposed on other grounds, the amphibians represent a transition from aquatic to terrestrial life, the modification of their developmental processes is a logical consequence. In reptiles, birds, and mammals, which are true terrestrial animals in development and as adults, the later stages have been modified, but the early stages still resemble those of the ancestral fish-like forms. It is not correct to say that the embryo of a reptile, bird, or mammal is a fish at any stage of its development; but it may be truly said that these embryos resemble the embryos of fishes at corresponding stages (cf. Fig. 5.22, p. 157). The statement that the animal "climbs the ancestral tree" in the course of its development is colorful but inaccurate. Many animals have in the course of their development structures that disappear or become greatly modified in later stages, and in many animals there is reason to believe that structures now transitory were formerly present and functional in the adult as well as in the embryonic stages. The fish embryo becomes an adult that is in many ways similar to the embryo, whereas the embryo of a terrestrial vertebrate advances beyond the fish-like stages of its embryogeny to develop the adult characteristics of the reptile, bird, or mammal. **Ontogeny**, the development of the individual, is not a repetition of **phylogeny**, the ancestral development; but certain structures that are reminiscent of ancestry may be found in embryos. As with adult anatomy, such facts of development are only to be expected if evolution has occurred; and they are inexplicable on any other grounds.

EVIDENCE FROM PHYSIOLOGY

All animals are alike in the basic capacities of metabolism, responsiveness, and reproduction, despite innumerable variations in the details of these processes. Therefore, we may reasonably suppose that all have descended from an ancestral protoplasmic system which possessed these basic capacities. Taken alone, this general uniformity of fundamental functions is less impressive than the many special cases of structural and distributional evidence; it does, however, serve to corroborate the evidence from other fields.

There is one very impressive line of specific evidence for evolution, from a field related to physiology. It has been pointed out that one aspect of the individuality of organisms is the specificity of the proteins which each organism produces. This protein specificity is the basis of the development of immunity to certain diseases in vertebrates, by the production of specific antibodies in the blood which react very precisely against foreign proteins. The immune reaction is one of the important mechanisms by which the body is protected against invasion by microorganisms, but when suitably stimulated a vertebrate produces antibodies against foreign proteins from any source. Developments in the field of **serology** have made available a technique, involving this capacity for immunization, that is very useful in the determination of degrees of interrelationship between different organisms. The technique and its application may be briefly described as follows. A rabbit is immunized against the blood proteins of a sheep, for example, by repeated small injections of proteins from the serum of sheep blood. Subsequently, the antibodies that have formed in the blood of the rabbit will react very strongly when in contact with sheep serum under controlled conditions. They will also react, though less positively, against serum proteins from the goat, the cow, the horse, or even man. The basis of the varying degree of reactivity is the varying degree of chemical similarity between the proteins of the different sera. It should follow that the blood proteins of closely related animals are more alike than those of distantly related forms; and the serological tests should make it possible to express in some quantitative terms the relative closeness or distance of the relationship.

Extensive tests of the serological technique have borne out its usefulness in this connection. The proteins of birds have proved to resemble those of other birds very closely, those of reptiles less closely, and those of amphibians not at all closely. Mammalian proteins are more similar to those of reptiles than to those of birds; human proteins react more strongly against proteins from other primates than against those from other mammalian types; and so on. In all animals the degree of similarity between the proteins of different groups, as shown by serological methods, confirms the degree of relationship between the groups inferred on the basis of other evidence. The technique is also applicable to purified protein extracts of the body fluids of invertebrates, and it has been demonstrated that the chemical affinities of chordates lie with hemichords and echinoderms rather than with any other invertebrate groups. This technique should prove very useful in resolving problems of phylogenetic affinities in many instances where other evidence is equivocal. The existence of degrees of chemical similarity between the proteins of different kinds of animals supports very strongly the inference of different lines of evolutionary descent from common ancestors.

EVIDENCE FROM DOMESTICATION AND SELECTIVE BREEDING

We need discuss only briefly another line of evidence bearing on the reality of organic evolution and on mechanisms which may have operated to bring it about. It is common knowledge that mankind began, long before the dawn of recorded history, to bring wild species of animals and plants under domestication, for his own convenience and welfare. The establishment of practices of agriculture and animal husbandry undoubtedly marked a most significant epoch in the cultural evolution of man, leading to the rise of settled population groups with a relatively dependable supply of foods and other necessities yielded by domesticated plants and animals. In the thousands of years during which these practices have developed, distinctive types of organisms have been produced, differing markedly from their wild forebears. In some cases it is possible to identify with reasonable certainty the original wild species from which all the domestic breeds appear to have descended; for example, the multitudinous breeds of domestic poultry are believed to have descended, by different genetic paths, from wild Asiatic jungle fowl. The differences among modern breeds, and between these and the ancestral types, could hardly be greater, considering that the process of domestication has been in progress during only a few thousand years.

Man has, in a very real sense, brought about evolution in the lines of animals and plants he has domesticated. He has done this by a constant process of **artificial selection**, choosing for breeding those types which from his own standpoint possessed desirable characteristics. By thus selecting some forms for survival and reproduction and rejecting others with less desirable traits, man has arranged for "the survival of the fittest"—the fittest in this case being the types that best suited man's needs of the moment.

Charles Darwin, in his famous works on evolution, argued very forcefully that evolution by this artificial selection appears completely analogous to evolution by **natural selection** in wild populations under conditions in nature, without man's intervention. If we substitute for man's standards of selection the many environmental factors which presumably operate in nature to select some types for survival while eliminating others, the comparison seems apt indeed. One fact has been raised in exception to this line of reasoning: whereas among natural populations different species can seldom be succesfully interbred, the "species" man has developed through artificial selection are usually interfertile. That is, no matter how vast the apparent differences may be between two kinds of dogs, or two kinds of poultry or cattle, these animals can usually be crossed to produce fertile offspring. This is one reason for referring to **varieties** or **breeds** of domestic animals, rather than calling them different species, even though their differences may be so extreme that if these types were discovered in nature they would probably be identified as different species. Undoubtedly, however, one of man's criteria for the preservation of types has been fertility, and continued interfertility may, like other characteristics, be the result of artificial selection in these domesticated stocks.

Until comparatively recently, the breeding of animals has developed as a skill, rather than as a science. Folk traditions and superstitions have guided the rule-of-thumb operations of breeders, and we still encounter references to "blood lines" which reflect the intuitive reasoning of the ancients that the blood of the individual was responsible for its characteristics. With the rise of genetics as an exact science, however, as discussed at length in Chapter 6, the application of its principles to selective breeding has removed much of the guesswork from planning and carrying out the production of new and superior breeds of domestic animals and plants. Heredity has without doubt played the same kind of part in natural evolution as it plays in selective breeding under domestication.

Summarizing the argument, we may state that the production of new types of animals and plants under domestication illustrates the kind and magnitude of changes which can occur in the characteristics of organisms with the passage of time. If this much evolution has occurred in a relatively short time under the selective guidance of man, it is only to be expected that much more impressive changes should have occurred in all living things during the extremely long period of time since life first appeared on earth.

Summary of Evidence for Organic Evolution

In summary, it may be repeated that evidence from many fields has led biologists to accept the evolutionary concept as the most logical explanation of the development of new kinds of animals. The geologic succession of animal types, as revealed in the fossil record, and their present geographical distribution, can be most reasonably interpreted according to the theory of organic evolution. Animals resemble each other in structure, in chemical composition, and in patterns of development in such a way as to indicate different degrees of interrelationship. The assumption that these facts reflect different lines of descent from common ancestry best explains the available evidence. Further evidence may be adduced from the production of new breeds of animals and plants under domestication. Very often the evidence is indirect or circumstantial, but it is so extensive, and so many lines of evidence support the same conclusion, that one cannot reasonably remain unconvinced of the reality of animal evolution.

Human Evolution

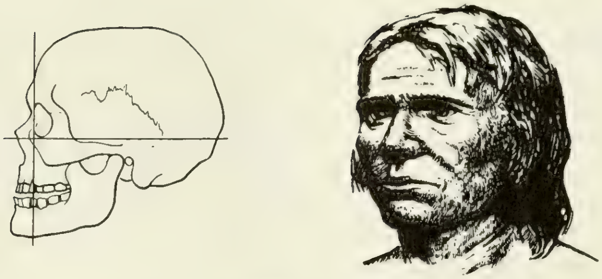
Man as a Primate. If the evolution of all other forms of life be accepted as a reasonable probability, it is illogical to exclude man from the universal process of organic evolution. Man's structure and embryonic development;

the classification of mankind in the family **Hominidae**, closely allied to the family **Pongidae**, or tail-less apes; the fossil record of prehuman and early human types; and the differences between the existing races of man—all point to an evolutionary process as the single reasonable explanation of the facts. Paleontological studies indicate that the order **Primates**, including man, apes, monkeys, and lemurs, arose from the generalized early mammalian stock. Fossil remains of prehuman races in more recent geologic time give evidence of the line of man's descent. Taken as a whole, the evidence for human evolution is entirely comparable with the evidence for the reality of animal evolution in general.

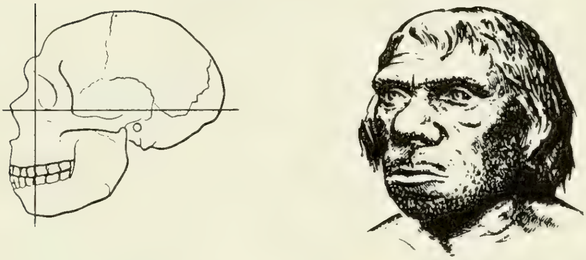
The structure of the human body is fundamentally like that of other mammals and resembles particularly closely the anatomy of members of the family Pongidae. This family includes the four types of tail-less apes: gibbon, orangutan, gorilla, and chimpanzee (see Fig. 18.35, p. 586). There is no essential detail of human anatomy that is not present in these apes, although the more erect posture of man has been correlated with characteristic specializations of the pelvis and viscera, the fore limbs, the foot, and other parts. The brain, of course, is the most distinctive feature of man; with few exceptions the brain of man is relatively larger than that of any other vertebrate. On the whole, the specialization of functions in the human brain exceeds that in any other mammal; but the structural and functional specializations of the human cerebrum are all approached, though not equaled, in the higher apes. The psychological characteristics of these apes also resemble those of man. The evidence justifies the conclusion that the ancestors of man advanced to articulate speech, to the development of greater powers of reasoning and insight, and to the perfection of the hands as organs of precise manipulation. Another line of descent, which produced the tail-less apes, failed to progress in these respects to the extent characteristic of the human evolutionary stock.

A large number of vestigial structures in adult anatomy, and of primitive characteristics in embryonic development, serve to link man to lower vertebrate forms. Vestigial gill slits and a fish-like circulatory system are formed in human embryos, as they are in those of other mammals. A tail develops in the embryo but becomes vestigial in the adult; at one stage of embryonic life the entire body is covered with a well-developed coating of hair. The great anatomist Wiedersheim enumerated at least 180 vestigial structures in the human embryo. There is no more logical explanation of these facts than the assumption that they indicate evolutionary descent from more primitive forms of life.

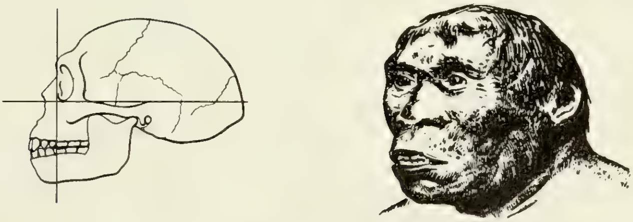
Evidence from Fossils and Artifacts. The remains of human and subhuman beings discovered in Africa, Java, China, Europe, and Palestine give further evidence of the evolution of man.. In many instances only fragments of skulls and of the larger bones have been found, but for certain types complete skulls and even entire skeletons have been discovered. The collections increase slowly year by year, but fossil remains of the earliest



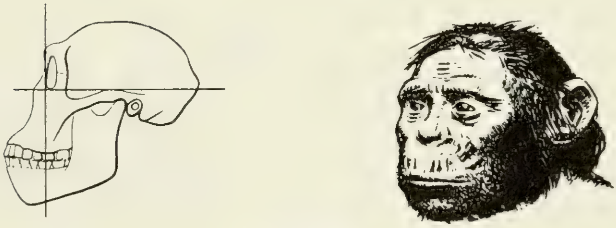
Cro-Magnon



Neanderthal



Pithecanthropus



Australopithecus

Fig. 20.8. Comparative aspects of the skulls and restored facial features of the man ape of Africa and early men of Europe and Asia. Note particularly the progressive changes in the proportions of the cranium and the lower jaw. (Adapted from E. H. Colbert, *Evolution of the Vertebrates*, copyright 1955 by John Wiley and Sons, Inc., printed by permission; *Australopithecus* skull after W. K. Gregory.)

human types will probably never form a complete series. In the early stages man's forebears must have existed not in large populations but in small groups, rather widely scattered. Fortunately, even in the absence of skeletal remains, human activities can be traced through discoveries of things that man made or used, and of places where he lived, either temporarily or during long periods. Artifacts, such as weapons and tools of stone or metal, crude or skillful drawings and carvings, the remains of campsites and dwellings, and so on, all give evidence of the manner of life, the cultural level, and sometimes the physical and mental development of early man. In certain caves which sheltered men for thousands of years, complete series of artifacts have been found which constitute a record of cultural evolution.

The distribution of fossil remains representing the earliest known stages in human evolution indicates that mankind's center of origin was probably in Asia or in Africa. Several examples of the early stages may be briefly discussed (Figs. 20.8, 20.9). *Australopithecus africanus*, the African ape man, is the earliest known type which is truly man-like. He was evidently of rather small stature and a fundamentally ape-like physique, but many features of the skeletal remains foreshadow later structural developments in the line of human evolution. *Australopithecus* is believed to have hunted baboons for food and to have killed them with crude stone weapons. The remains of *Australopithecus* have been assigned to a period about 1,000,000 years B.C. Somewhat later, about 900,000 to 800,000 B.C., Java was inhabited by a group of still more man-like primates, assigned to the species *Pithecanthropus erectus*. Other than the physical characteristics which can be inferred from the relatively few fossil skulls and jawbones, little is known of this species. Near Peking, China, however, more abundant skeletal and cultural remains have been discovered which date from about the time of the Java ape man. These were originally assigned to a new genus, *Sinanthropus*, but continuing studies have revealed so many similarities between *P. erectus* and the ancient Chinese men that their inclusion in the same genus seems justified. *Sinanthropus pekinensis* is therefore now referred to as *Pithecanthropus pekinensis*. Whatever their correct scientific name, these men inhabited caves during a warm period following the first of the great Pleistocene glaciations; they hunted numerous kinds of contemporary wild animals, fashioned rough stone tools and weapons, and used fire. The skulls of *P. pekinensis* often show signs of having been roasted and broken open, presumably to extract the brain, which may indicate that these people were cannibalistic.

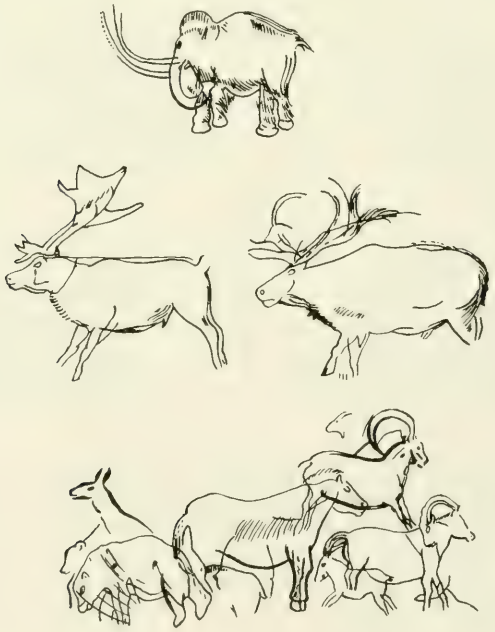
In response to the same factors which governed the spread of other organisms from their centers of origin, early man probably migrated in small groups away from the ancestral homeland. There is evidence that men reached Europe during the same warm interglacial period which saw the rise of *Pithecanthropus* in China. The Pleistocene was one of the most dramatic epochs in the geologic history of the Northern Hemisphere. Four separate times, between about 1,000,000 and 15,000 B.C., great glaciers slowly spread southward on all the northern continents, and then slowly receded northward.

GLACIAL STAGES		TIME and CLIMATE	MAN	
NORTH AMERICA	EUROPE			
POST-GLACIAL		HISTORIC 5,000 B.C.	Modern races of man	*Homo sapiens*
WISCONSIN	WÜRM	15,000 B.C. COLD	Cro-Magnon (Europe) Folsom man (N. Amer.) Sandia man (N. Amer.) *Homo soloensis* (Java)	
III INTERGLACIAL		125,000 B.C. WARM	*Homo rhodesiensis* (Africa) *Homo neanderthalensis* (typical) Europe	"NEANDERTHALOIDS"
ILLINOIAN	RISS	275,000 B.C. COLD		
II INTERGLACIAL		375,000 B.C. WARM		
KANSAN	MINDEL	675,000 B.C. COLD		
I INTERGLACIAL		750,000 B.C. WARM	*Homo heidelbergensis* (Europe) *Pithecanthropus* (China) *Pithecanthropus* (Java)	
NEBRASKAN	GÜNZ	900,000 B.C. COLD		
PRE-GLACIAL		1,000,000 B.C. WARM	*Australopithecus*	

Fig. 20.9. Divisions of the Pleistocene "Ice Age" and the approximate time relations of various prehuman and human types. (Adapted from O. D. von Engeln and K. E. Caster, *Geology*, copyright 1952 by McGraw-Hill Book Co., Inc., printed by permission.)

During the interglacial periods the climate was warm; there were extensive forests, and the fauna of Europe included the mastodon, the mammoth, the woolly rhinoceros, and the saber-toothed tiger. Man came to Europe as a puny competitor of these mighty animals but succeeded in developing the cunning and prowess necessary for survival. An interesting series of skeletal remains, and much more numerous collections of artifacts and cultural relics, enable us to reconstruct the physical characteristics and to some extent the lives of these primitive men.

A large jawbone, found near Heidelberg, represents the oldest known human type in Europe. It has been assigned to the species *Homo heidelbergensis;* it may be noted that this is the first of the progenitors of modern man considered sufficiently advanced to be placed, with modern man, in the genus *Homo*. During subsequent ages, Europe was peopled by a race which either descended from men of the Heidelberg type or arrived in a later wave of migration from elsewhere. These constitute what has been called a generalized Neanderthaloid stock, because they show in some degree the special characteristics of Neanderthal man (*Homo neanderthalensis*), a species named from remains related to a much later geologic period. The generalized Neanderthaloids ranged widely over Europe; their skeletal and cultural remains have been discovered in Spain, France, Central Europe, the Crimea, Palestine, and other regions. They were a hunting people, and groups of them occupied caves in certain areas for extended periods of time. The skeletons show that these men were powerfully built, with a rather



stooping posture and short, muscular arms and legs. The characteristics of the skulls indicate somewhat ape-like facial features, with beetling brow, prognathous mouth, and receding forehead and chin. The paleoanthropological evidence is still too scanty to permit a clear statement of the antiquity of the generalized Neanderthaloids, or of their relationship to modern man. However, some authorities incline to the belief, at least provisionally, that they date from the Middle Pleistocene in Europe. There appears to be nothing in the characteristics of the generalized Neanderthaloids to argue strongly against including them, with modern man, in the species *Homo sapiens*. The true or classical *Homo neanderthalensis* appears, on the other hand, to represent a relatively small and isolated group which originated from this generalized stock just prior to the onset of the fourth Pleistocene glaciation, about 125,000 B.C., and became extinct before its close at about 15,000 B.C.

The earliest undoubted members of our own species, known as the men of Cro-Magnon, supplanted the earlier Neanderthaloids in Europe in postglacial times. They were tall, erect, and evidently fine physical specimens and were probably relatively intelligent. The caves which they occupied for long periods, or which they may have used for ceremonial purposes, show a variety of surprisingly artistic and realistic paintings and carvings of men and animals (Fig. 20.10). From these cave paintings alone it would be possible to draw up lists of the larger animals contemporaneous with Cro-Magnon man in Europe; many of these animals have since become extinct or

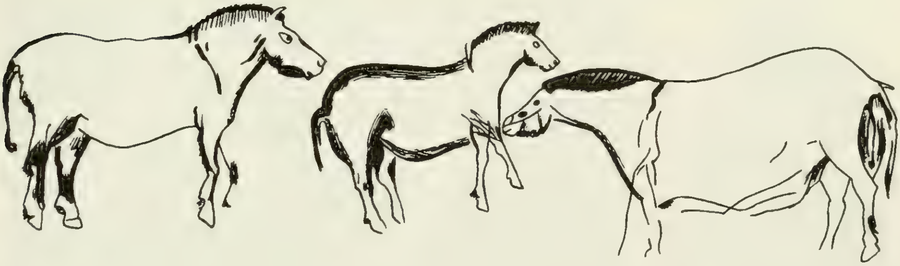


Fig. 20.10. Specimens of cave art from the cavern of Les Combarelles, France. Discovered in 1901, these surprisingly realistic carvings and paintings date from late in the Old Stone Age, about 20–25,000 B.C. In addition to the horses (of which three kinds can be recognized in the cave), such other forms as cave bears, reindeer, ibexes, and mammoths are shown, all of which are now extinct or no longer occur in this part of Europe. (Redrawn from H. Breuil, 1926, *Natural History*, vol. 26, printed by permission.)

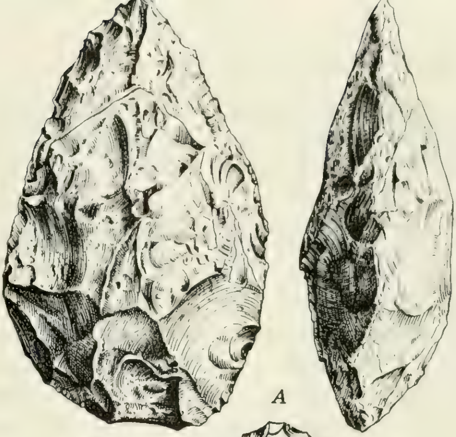
no longer occur in Europe. Cro-Magnon man was either displaced or absorbed by the later progenitors of modern Europeans.

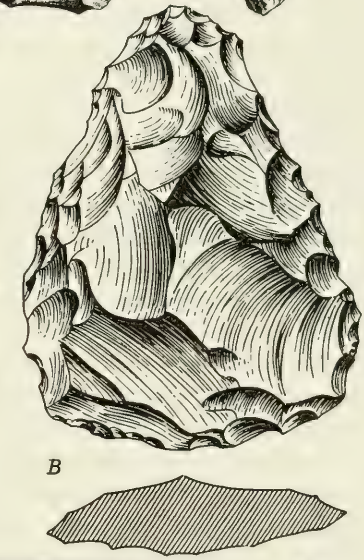
The history of mankind in America, though much longer than was once supposed, covers a comparatively brief span of time. The earliest human immigrants apparently reached North America from Asia by way of a land connection at Bering Strait. They arrived prior to the last Pleistocene glaciation; there is an abundant record of long human occupation of some of the Aleutian Islands and in the Point Barrow region of Alaska. Various discoveries in different parts of the American continents indicate that men spread southward and eastward from the ancient Bering gateway, and that they were well established in both North and South America by 25,000 B.C. Stone arrow or lance points of a distinctive type, fashioned by a race of hunters named Folsom man, have been found widely scattered in the United States (Fig. 20.11). Many of these points, discovered as far east as New York and Pennsylvania, were probably carried eastward by later peoples; their distribution does not necessarily coincide with the area occupied by Folsom man. However, in undisturbed sites in Colorado and New Mexico, the Folsom points, associated with the bones of extinct mammals, give evidence of the presence of these people at a period ranging from 10,000 to 12,000 years ago. Folsom man was not the earliest human inhabitant of the southwest; deposits in the floor of the Sandia Cave, in New Mexico, have yielded the distinctive stone weapons of a culture dating from possibly 20,000 B.C. These are overlain by barren deposits, and these, in turn, by layers containing Folsom artifacts. The barren layers are believed to represent long periods when the cave was unoccupied, probably during the period of climatic upheaval associated with the retreat of the last continental glacier in this area. Another nomad-hunter culture apparently existed in the southwest at about the same period as that represented by the early Sandia remains, and may have been much older. This is known as the Clovis culture, again recognized by distinctive stone weapons; materials from New Mexico date from 12,000 to 16,000 years ago, while similar Clovis remains from a campsite recently unearthed in North Texas have been declared older than 37,000 years. If this dating is accurate, the Clovis group represents the oldest known North American men.

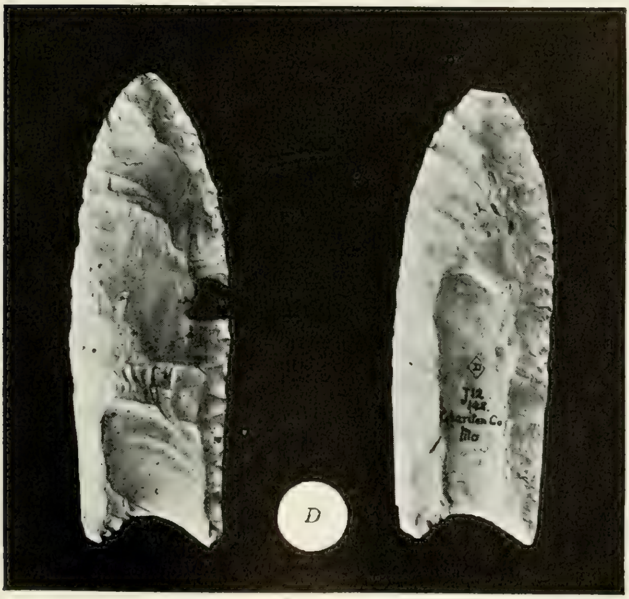
Although many campsites, artifacts, and burned animal bones from early American cultures have been found, there have been no discoveries of actual human skeletal remains of the earliest Americans. It is unlikely, however, that in their physical characteristics these people differed markedly from the later American Indians; *Homo sapiens* must have been established in Northeast Asia much earlier than the time of the earliest Bering land-bridge migrations. There is abundant evidence that the American Indians are remote descendants from an Asiatic stock, either through the Clovis, Sandia, and Folsom people or from successive later waves of migration.

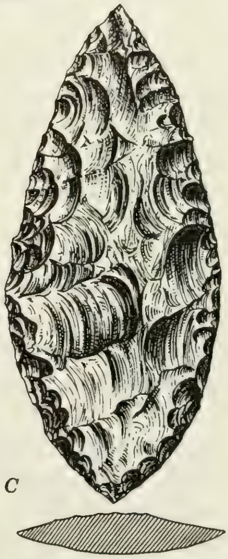
Although the fossil record of mankind is extremely fragmentary, enough physical and cultural remains are available to make it abundantly clear

Fig. 20.11. Stone artifacts from Europe and North America. *A*, face and profile views of a hand ax typical of the Acheulian cultural epoch of Europe, centering about the second interglacial stage of the Pleistocene; note that the stone is finished on one side only. *B*, chipped stone implement of the Mousterian culture, spanning the third interglacial stage; such implements were used by Neanderthal man. *C*, "laurel leaf" point of the Solutrean culture which flourished in parts of Europe during the fourth or Würm glaciation. The shaded figures with *B* and *C* show the stones in cross section, for comparison of thickness. *D*, two Folsom points from North America, similar in method of manufacture to the finely finished Solutrean points from Europe, which were thinned and shaped by flaking. (*A*, *B*, and *C*, after J. Andrée, from L. F. Zotz, 1951, *Altsteinzeitkunde Mitteleuropas; D*, photograph courtesy American Museum of Natural History.)









that man has undergone an evolutionary process comparable with those of other forms of life.

Theories Concerning Organic Evolution

Organic evolution as an historic fact is attested by the evidence outlined in the preceding section. We may now examine the more important theories concerning the factors that have conditoned organic evolution. Most notable among these are Lamarck's Theory of the Inheritance of Acquired Characteristics and Darwin's Theory of Natural Selection. We shall also discuss briefly conclusions from recent studies in genetics and ecology. Any comprehensive theory must take into account both internal and external factors. Among internal factors are the phenomena of heredity, variation, reproduction, and development; external factors include all environmental conditions that affect individuals and populations.

Lamarck's Theory of the Inheritance of Acquired Characteristics: *Historical.* The works of Lamarck (1744–1829), written principally during the first quarter of the nineteenth century, postulated that evolutionary changes are conditioned by the inheritance of characters acquired during the life of the individual. Lamarck built this theory upon the earlier works of another Frenchman, Buffon (1707–1788), who had previously stated the concept of evolution as opposed to special creation. Many of Lamarck's statements, examples of which will be given later, appear fanciful in the light of modern knowledge. His essential claim that characters acquired by an individual during its lifetime are inherited by its offspring, and thus produce evolutionary changes, has never been substantiated. Nevertheless, the publication of Lamarck's theory served to focus attention on the subject of organic evolution.

Explanation of Lamarck's Theory. In its modern form the Lamarckian theory states that during the life of an individual new characters can be acquired by use or disuse of parts, and also by the direct effects of the environment on somatic cells. It is a familiar fact that the use of muscles increases their development; and the old adage "practice makes perfect" finds many illustrations in the refinement of neuromuscular coordination through prolonged repetition of actions. Conversely, disuse leads to deficiency or even complete loss of function, as illustrated by the fanatic of India who holds a limb in one position until it cannot be moved, and by many other examples. Such effects of use and disuse, and many effects of the environment on the individual, are known technically as **acquired characters.** There can be no doubt that they occur; the Lamarckian theory holds, however, that such effects constitute heritable variations and thus condition evolution.

The process supposed to occur in nature may be illustrated by citing some of Lamarck's own examples, in somewhat modified terms. If swift-footed animals, such as deer, have acquired their fleetness by running from their enemies, it follows that each generation has been forced to exert itself to the utmost, like an athlete always in training for a race, and that the effects of such training in each generation have been passed on to the next. Thus, fleetness has gradually increased up to limits determined by the nature of the organism. Similarly, the fleetness of the pursuing wolves may have been increased generation after generation. Animals living in cold climates, where the environment stimulates a heavier growth of hair or the formation of more fat beneath the skin, are believed to transmit these characters by heredity; their descendants at length reach the state seen in arctic forms. Many other examples of this line of reasoning could be cited, such as the degeneration of the eyes in cave-dwelling animals, the increase in neck length in giraffes, and so on. Lamarck also believed that the animal in some way "willed" or determined the course of its evolution.

Present Status and Critique. If it could be shown that the effects of use and disuse and the direct effects of environment upon the individual are actually inherited, there would be little criticism of Lamarck's theory. Many attempts have been made to obtain specific evidence, but none of the alleged examples has held up under subsequent investigation. Experiments involving the destruction of parts, such as the amputation of tails in mice during many generations, and experiments in the functional stimulation of various parts, and in the effects of changed environment, have given negative results. The organism may develop new characters in a new environment, but when it is returned to the original environment, the alterations do not persist. In general, it may be said that experimentation has failed to support the Lamarckian theory; it appears that characters acquired by the individual during its lifetime, in the manner postulated by Lamarck, are not heritable.

A theoretical objection may be raised to the entire idea of the inheritance of such acquired characters. A new individual develops not from its parents' somatic cells but from their germ cells; and germ cells are in most cases set apart at an early stage in development and are little influenced by what happens to the somatic cells in the normal activities of the animal. The Lamarckian scheme would require that a change in somatic cells of a part of the body be transmitted to the germ cells, in such a way as to affect whatever it is in the germinal material that conditions the development of this specific part. To use a homely if old-fashioned illustration, a blacksmith's son inherits his arms not from his father's arms but through his father's and mother's germ cells; and it is the germ cells that must be changed before any modification can be inherited. The facts of genetics, embryology, and physiology give virtually no theoretical support to the Lamarckian doctrines and thus confirm the negative results of experimentation.

Darwin's Theory of Natural Selection: ***Historical.*** The teachings of Lamarck regarding evolution attained considerable popularity during the early nineteenth century but were apparently overthrown by Cuvier (1769–1832), the greatest zoologist of his day, who opposed the concept of evolution. In 1830, a year after Lamarck's death, a debate was held in the French Academy in which Saint-Hilaire (1772–1844) upheld the Lamarckian doctrines against Cuvier. Despite his opposition to the idea of evolution, Cuvier had been forced to admit the differences between animals of the past and those of the present, differences which could not exist if animals had been originally created in their present form and had not changed. Therefore, Cuvier had espoused the Doctrine of Cataclysms, which assumed not one but a series of creations, each followed by a cataclysm that destroyed all life. By supposing that each successive creation was on a higher level than the preceding, it was possible to explain the succession of types appearing in the fossil record. But the work of the geologists, culminating in Lyell's *Principles of Geology* (1830), showed that there was no evidence for cataclysms. The period between 1830 and 1859, during which Darwin was engaged in the studies summarized in his book, *The Origin of Species*, was one of relative quiescence for the evolutionary theory. There was much popular interest in the subject, however, as shown by the large sales of Robert Chambers' book, *The Vestiges of Creation* (1844). Cuvier won his debate with Saint-Hilaire, but in 1830 the case was already settled in favor of evolution, as subsequent developments showed.

Charles Darwin (1809–1882) began his studies 20 years before the publication of his famous volume. The fact that he was interested in determining whether species originated by creation or transmutation (that is, evolution) shows that the question was then under discussion. The idea seemed new in 1859 only because the evidence was so ably presented by Darwin and so rapidly accepted by scientists and others. From our present point of view, it is difficult to understand why biologists failed to recognize at an earlier date the evidence for organic evolution—evidence that had been steadily accumulating since the work of Buffon (1749), and that was sufficient to justify acceptance of the concept 20 years before 1859. Nevertheless, Darwin deserves his fame because it was he who brought about the acceptance of the evolutionary doctrine. His *Origin of Species* was a masterful summary and extension of the evidence for organic evolution as an historic fact. Its publication marked the beginning of a new epoch in human thought, as well as in biological science.

Explanation of Darwin's Theory. In addition to bringing together and extending the evidence for the reality of organic evolution, Darwin proposed as a major factor in the origin of species, and hence in evolution, what he called **natural selection**. The principles of natural selection were independently recognized by Alfred Russel Wallace in 1858. As conceived by Wallace and Darwin, these principles may be summarized as follows. Organisms possess an innate capacity for unlimited increase in numbers, but under normal conditions populations remain approximately stationary. The limitations on increase reflect a struggle for existence on the part of the organism. In every population, random heritable variations occur in the characteristics of organisms; these are not imposed or evoked by any action of the environment or of the organism but appear spontaneously and in all directions. By chance, some of the variations will be advantageous in the struggle for existence, and others will be unrelated to survival or will be detrimental. Natural selection involves the action of the environment in selecting for survival those forms which, by chance, are best adapted to environmental conditions, and in eliminating those less well adapted. This results in the **survival of the fittest,** in terms of any specific environment. If the characteristics of the environment change, a new process of selection begins and a new group of organisms is selected, with modifications in adaptation to the changed environment.

In *The Origin of Species*, Darwin cites example after example of observations supporting these principles. In his accounts of the environmental relationships of organisms, Darwin anticipates many of the important generalizations that have arisen from modern ecological studies. Much of our discussion in Chapter 19 states in specialized terminology the principles and conclusions that Darwin adduced in support of his theory of evolution. Consider, for example, Darwin's concept of the "struggle for existence." Since the capacity for reproduction is restricted by checks upon increase, relatively few of the individuals that begin life in any generation will reach maturity. Each individual, therefore, must engage in a fight for survival. As Darwin conceived it, this struggle for existence is seldom an actual conflict, although this may be involved when animals fight with one another for mates or for food. He thought that the struggle would be most acute between individuals of the same species, since these compete for the same conditions of life; or between different species using the same food, as when insects devour the food of grazing mammals. It is important to bear in mind that Darwin used the term **struggle** in a metaphorical sense. In the vast majority of cases there is nothing that can be called a struggle in the sense of actual conflict. Metaphorically, however, it can be said that the trees of a forest, competing for soil nutrients and for light, "struggle" to exist or "fight" for life. Darwin concluded that such a struggle, in one or more of its aspects, is ever-recurring for all organisms, although it is intermittent and may not act for considerable periods in the life of any individual. The elements of Darwin's struggle for existence are implicit in the broad modern concept of **competition** (pp. 609–614).

The modern views of variation and heredity have been presented in Chapter 6. Heredity has been defined as the tendency of individuals to resemble their ancestors and relatives, and variation as the tendency of individuals related by descent to differ in various ways. The two are intimately connected as different expressions of the reproductive and developmental processes. Darwin observed that the members of species varied, and he believed that many of these variations, small though they might be in many instances, were inherited. He was interested in heredity and variation as such and studied them intensively; but so far as they concerned natural selection, it was not necessary to explain them. His argument was: **given** heritable variations and the reproductive capacities of organisms, a struggle for existence and natural selection inevitably follow.

Among inherited variations of many sorts, some will be of value to the individual in its struggle for existence; that is, some will have survival value. According to Darwin, if the members of a species of plant varied in their ability to resist frost, those that were sufficiently resistant would survive temperatures that would be fatal to the great majority. Inheritance of the variation by the next generation would follow, and such a process of selection, repeated through many generations, would produce a population better fitted to meet this particular condition of existence. Thus, evolution might occur by modification of this feature of the organism in a manner to suit a changing environment or to enable the species to extend its range northward. In a similar manner, heritable differences in resistance to a disease would produce a more resistant race; if wits were more important than strength, selection would develop a more cunning type. If concealment were of survival value, coloration and other features that tend to make the individual resemble its surroundings would be at a premium and therefore selected. Darwin called the process by which useful variations were sorted out natural selection, because it resembles the artificial selection practiced by breeders of animals and plants in picking individuals that please the fancies or necessities of man. Herbert Spencer called the process survival of the fittest, because the individuals best fitted to the conditions of existence were the survivors in the struggle for existence. In terms of genetics, the rate and extent of any evolution thus directed by selection depend on the occurrence of heritable variations that can be acted on by selection. Minor fluctuations in the expression of a characteristic are of no importance, since they are not inherited.

In our ecological discussions we considered, for the most part, short-term environmental changes and their effects on the populations of particular habitats. Yet great changes also occur over very long periods of time, as when continents are made and unmade by geologic evolution, or when profound climatic changes occur, such as the advent of an Ice Age or the change from forest to desert conditions. These are less important in the day-to-day activities of animals in a community than environmental changes which may seem insignificant in comparison. The introduction or destruction of a plant upon which various animals feed may produce far-reaching changes in the environmental conditions of a given species. New enemies entering a district may bring new standards of selection; new parasites or pathogenic microorganisms may put a premium on qualities that have not hitherto been selected. In the interplay of forces it is possible that conditions, and therefore selection, may remain stable for long periods, or that selection may suddenly take new directions. Changes of many sorts are conceivable within the limits of the selection pressure and the heritable characters available for selection. In terms of natural selection, the environment may be compared to a sieve that selects individuals presented to it but does not determine their nature. As long as the sieve remains unchanged, it allows the same kind of individuals to pass its meshes—to survive. But the sieve may change and may then select new kinds of individuals for survival. Evolution now in one direction, now in another, is therefore perfectly possible.

It should be reiterated that the theory of natural selection, as set forth by Darwin, does not attempt to explain the nature of variation and heredity. Selection is viewed as a directive rather than a creative factor in evolution. Also, selection cannot be thought to control or direct the evolution of non-adaptive or non-useful characters, unless these are linked in heredity with characters that are adaptive.

Present-Day Concepts of the Mechanism of Organic Evolution

The major outlines of Darwin's theory of natural selection stand as a recognized major contribution in the history of evolutionary thought. The soundness of Darwin's conclusions, resting on innumerable observations patiently fitted together into a logical pattern of interpretation, is the more impressive when it is realized that they were drawn in complete ignorance of the basic mechanisms of heredity, and without the significant data yielded by modern experimental work in the environmental relations of animals and plants. In the years between 1859 and 1900, no biological topic was more widely discussed than that of natural selection; the idea of the struggle for existence was particularly questioned. Although numerous biologists busied themselves collecting information that might be brought to bear on the evolution question, there appear to have been virtually no persistent investigations by experimental methods to establish the validity of Darwin's ideas, and his critics did not present any strong evidence against the theory. With the gradual rise of the science of genetics after 1900 and the later application of its principles to studies of population phenomena, and with the development of ecology as an experimental science that has demonstrated the competitive basis and the reality of the struggle for existence, Darwin's ideas have taken their place as the keystone of present-day evolutionary theory.

A major contribution from the field of genetics has been the understanding that mutations constitute the "random heritable variations" postulated by Darwin, and that the establishment of new sets of inherited characteristics in a population is the basis of evolutionary change. Although the production of mutations is understood in a general way, and the general selective action of the environment can be appreciated, it is difficult to determine precisely when or where a new species is established, in a continuously changing group of organisms. An answer to this question depends, of course, on how we define a species. One particularly dynamic view of this important concept holds that a species is the stage, in a process of continued evolutionary divergence, at which the members of formerly freely interbreeding populations have changed to such an extent that they no longer successfully interbreed. One of the most significant factors conditioning the establishment of new genetic combinations, and thus contributing to the formation of species, involves various forms of **isolation.**

Free interbreeding tends to promote uniformity in a population. Therefore, some degree of isolation is necessary for new combinations of characteristics to become established and to form steps in evolutionary change. From the standpoint of genetics, the conditions in nature that effect such isolation are many and varied. For example, the production of hybrid zygotes may be prevented by ecological, seasonal, or geographical factors operating in such ways that adult members of different populations never encounter each other. This effectively prevents interbreeding and the consequent exchange of heritable characteristics between the groups. A classical example of ecological isolation is furnished by snails of the family **Achatinellidae,** found in the Hawaiian Islands during the 1850's by John T. Gulick (1832–1923). Snails of this family live in trees. Since they cannot travel any distance over a land surface devoid of shade or moisture, their distribution is restricted. Along the sides of the principal mountains on the island of Oahu there are small valleys in which these snails find suitable habitats. But the snails cannot easily cross the ridges between adjacent valleys, or the crest of the mountain; neither can they move out upon the plain below. A population that becomes established in any valley tends to remain isolated from those in other valleys as long as similar climatic and topographical conditions prevail. At the time of Gulick's original collections, he found that almost every valley had its particular species or subspecies, differing in size, color, and shape of shell. More recent collectors have reported a species that seems to have been restricted to a single tree, sufficiently isolated to prevent migration and contact with other groups.

It is difficult to regard differences of the kind shown by these snails as useful or adaptive, and thus as having a selective value in the environments observed; the environment in all the valleys appears to be essentially uniform. The varied characteristics of these populations of snails may be interpreted as non-adaptive and hence as having no significance in the process of natural selection. Their appearance may best be accounted for on the basis of the isolation of the breeding populations. Under such conditions of isolation, each population evolves independently of the others, and because of the somewhat different inviduals originally present or subsequently appearing at random in the different groups, all are likely to evolve in different directions. Genetically speaking, each population consisted originally of individuals with certain combinations of genes, no two populations being identical. The mere sequence of generations produced, by random assortment and recombination, increasingly varied gene complexes in the different populations, and mutations continued to occur at random in each of the groups. From these possibilities, in accordance with the laws of probability, different types, and hence evolutionary changes, resulted. Even from populations made up originally of genetically homogeneous and freely interbreeding individuals, separate small groups maintained in isolation for long periods of time would undoubtedly in the long run develop into distinct species, just as these snails of Oahu have done.

There are many other examples of the effectiveness of such geographical or ecological isolation. Sometimes, isolating mechanisms operate even when adult forms occur together. These mechanisms may be **psychological,** as when for any reason males and females of the two forms fail to show sexual interest in each other; they may be **mechanical,** involving a physical incompatibility which prevents copulation; or they may be **physiological,** involving failure of spermatozoa to reach the ova to effect fertilization. In still other forms, hybrid offspring are inviable, dying at some stage of development before they reach sexual maturity. Hybrids that survive to the stage at which reproduction occurs in the parent species are commonly incapable of producing viable gametes. Mechanisms of isolation, particularly those involving reproductive functions, are undoubtedly related to the establishment of **incipient species** by the formation of subspecies or lesser groups that breed successfully only among themselves; at later stages they are important in maintaining the boundary lines between established species.

This origin of incipient species must be recognized as the next stage in evolution after the appearance of heritable variations. It is possible to understand, even without an extended explanation of the genetic principles involved, that the appearance of heritable variations (changed gene complexes) and their perpetuation, first in small groups of individuals and then in larger groups which eventually become species, are the first steps in evolution. Thus, one species may arise from a pre-existing species, and a third from the second, and so on; and great evolutionary changes may occur in the course of time. Since the origin of life on earth, there has certainly been enough time to permit the operation of such mechanisms of evolution. In the last analysis, as Darwin clearly recognized, accounting for the origin of species is the key to an understanding of the evolutionary process.

It has been argued that this view of evolutionary mechanisms and of the importance of natural selection is inadequate, because it fails to explain many lines of evidence that seem to indicate that mutations and subsequent evolutionary changes do not occur at random and in all directions. The evidence often cited involves evolutionary sequences in which changes all seem directed toward some pre-determined end form, and in which it is possible to detect steady trends, such as increase in size and the consistent development of special characteristics which appear to be non-adaptive or without obvious selective value to the organism. From the standpoint of genetics, it is argued that the occurrence of mutations is not a chance phenomenon, because, for example, the same mutations occur repeatedly in populations of organisms. All this evidence has been taken to indicate the existence of what has been termed "plan and purpose" in evolution.

It must be borne in mind, however, that living systems involve specifically organized and delicately balanced functional mechanisms, about which the structural features are organized. Such systems obviously cannot be changed in completely random ways, or with any large deviations from the normal, without disrupting their fundamental conditions of equilibrium. The characteristics of organisms are thus bounded at all stages by rather finite limits, and any changes beyond these limits are detrimental to the organism. To this extent, then, heritable variations or mutations cannot occur at random. For any particular kind of organism, the number of directions in which change can proceed, consonant with continued life, is limited; and only such changes as may proceed in these directions can persist and give rise to new evolutionary stocks. Changes in some directions may, under certain environmental conditions, be of survival value to the organism and thus may be selected for preservation. Changes in other directions may appear to be non-adaptive, or to have no demonstrable survival value; these may persist because they are "neutral," because selective processes do not operate to eliminate them, or because they have become genetically linked with selected characteristics. This may account for the persistence, through long evolutionary sequences, of such apparently non-adaptive characteristics as overgrown spines and large, complicated shells among some of the invertebrate groups. Changes which are adaptive, and thus selected, in some stages of the history of a group may, under changed conditions, become neutral; or they may actually become detrimental and so contribute to the eventual extinction of the race. The evolution of non-adaptive characteristics, and the evidence that evolution is not a completely random process, may be explained by some such reasonable considerations.

Summary

The history of organisms, as indicated by the data of biology and other sciences, has involved gradual processes of change from some primitive form or forms of life. How and when these primitive forms originated on our planet are matters of speculation. The place of origin was probably in the primordial seas, and the time must have been some period after these waters had cooled sufficiently to permit living systems to exist. Evidence drawn from a wide range of observations and experiments demonstrates the reality of the evolutionary changes that have produced existing forms from this primitive ancestry. The facts of distribution, both geologic and geographic, and the facts of anatomy, embryology, and physiology can be most reasonably explained in accordance with the theory of organic evolution. The strength of this evidence is in its extent and diversity. Any other explanation of the data is a violation of common sense as well as of scientific reasoning. Much of the evidence is indirect and circumstantial, but more direct and experimental evidence, based on studies in plant and animal breeding, genetics, and ecology, confirms the conclusion that the only reasonable explanation for a vast array of facts is provided by the theory of evolution. Mankind is not exempt; the evidence clearly indicates that man originated as an evolutionary offshoot from the mammalian stock that produced the higher apes, and that man's more remote ancestry is in common with that of all other vertebrates.

With the historic fact of organic evolution thus established, and its general course indicated, the factors that have conditioned evolution remain to be explained. A full explanation of these factors has not been accomplished, but it is evident that variation and heredity are the beginning of evolutionary modification; that isolation of incipient stages in small groups is important; and that natural selection has directed evolution along pathways which fitted the organism to its environment. These have certainly been among the factors conditioning organic evolution. No case has been established for the Lamarckian theory; the principal aspects of Darwin's theory of natural selection, interpreted in the light of modern knowledge of genetics and ecology, serve as a basis of a reasonable theory describing the probable mechanisms of evolutionary change.

As a fundamental generalization of biological science, only the Cell Theory can rank with the Theory of Organic Evolution. Developing somewhat earlier in the history of biology, the growth of the Cell Theory was correlated with great advances in our understanding of biological science and in its practical application. Attaining prominence and widespread acceptance some years later, the Theory of Organic Evolution has had a similarly universal impact on biological thought and interpretation, and its importance continues to grow with the accumulation of new evidence from many areas of biological science.

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GLOSSARY

This glossary is not a complete dictionary of zoological terms or even of all such terms used in this book. Words that are used in a limited part of the book are defined where they occur, and the student is referred to the Index in such cases.

A-. Combining form, meaning "without."

ABDOMEN. That part of the trunk of a vertebrate which is posterior to the thorax and separated from it by the diaphragm, and which contains that part of the coelom known as the abdominal or peritoneal cavity. In the arthropods, the posterior division of the body.

ABORAL. Opposite the mouth.

ABSORPTION. The taking in of soluble foods by the circulating fluids.

ACOELOMATE. Animals that are bilaterally symmetrical and triploblastic but have no body cavity of any kind between the gut wall and the body wall.

ACQUIRED CHARACTER. A phrase used as a synonym for somatic variation or fluctuation in Lamarck's Theory of the Inheritance of Acquired Characters. Since all the characters of any individual are acquired as the zygote develops, the phrase is an unfortunate one.

ACTIVATION. The initiation of development, usually the result of the penetration of an ovum by a spermatozoon.

ADAPTATION. Any modification of an organism that better fits it for existence in its present environment or enables it to live in a different environment.

ADDUCTOR MUSCLE. A muscle that draws a part toward a central region or median line.

ADSORPTION. The accumulation of particles on a surface.

AFFERENT. Carrying to or toward a given region. *Cf.* **EFFERENT.**

AGAMETE. Any single cell, other than a gamete, that can reproduce the organism.

AIR TUBES. Tubes conveying air to the lungs in vertebrates and from the spiracles to the cells in certain arthropods.

ALBUMEN. The white of the reptile's and bird's egg, surrounding the yolk, or zygote, and used as food by the embryo.

ALGAE (*sing.* **ALGA**). A group of green plants with relatively simple organization.

ALLELOMORPHS. Genes located in comparable positions on homologous gene strings but producing alternative effects in a given character; for example, gene *A* might condition the appearance of black hair, and an allelomorph, gene *a*, might condition the appearance of white hair.

ALTERNATION OF GENERATIONS. *See* **METAGENESIS.**

ALVEOLUS (*pl.* **ALVEOLI**). A small cavity, such as any one of the minute air sacs in the mammalian lung or a secreting portion of an alveolar gland.

AMBULACRAL. Pertaining to the rows of openings through which the tube feet of echinoderms are extended; hence, ambulacral system of which the tube feet are a part.

AMINO ACIDS. Organic acids containing one or more amino groups ($-NH_2$); units of which proteins are composed.

AMITOSIS. Direct nuclear division, without the formation of chromosomes. *Cf.* **MITOSIS.**

AMOEBOID. Pertaining to or resembling an amoeba; usually used with respect to locomotion.

AMPHIBIOUS. Living both on land and in water.

AMPHIMIXIS. The fusion of the nuclei of the two gametes that give rise to a zygote.

AMPULLA (*pl.* **AMPULLAE**). A flask-shaped structure.

ANABOLISM. Collective term for synthetic reactions of cellular metabolism. *Cf.* **CATABOLISM.**

ANAEROBIC. Able to live in the absence of free oxygen.

ANALOGY (*adj.* **ANALOGOUS**). Correspondence in function. *Cf.* **HOMOLOGY.**

ANATOMY. The science of the structure of animals as revealed by dissection; gross morphology. *Cf.* **HISTOLOGY.**

ANIMAL HEMISPHERE. That half of a telolecithal egg in which the nucleus is located and which contains less yolk than the vegetal hemisphere.

ANIMAL POLE. That point on the surface of an egg at which the polar bodies are formed; one end of the egg axis. *Cf.* **VEGETAL POLE.**

ANISOGAMETES. Gametes of unequal size that unite in pairs. *Cf.* **ISOGAMETES.**

ANISOGAMY. Fusion of gametes of unequal size. *Cf.* **ISOGAMY** and **FERTILIZATION.**

ANTERIOR. Pertaining to or situated toward the head; the end which is directed forward during locomotion; the end which contains the mouth. *Cf.* **POSTERIOR.**

ANTHROPOLOGIST. One who studies the science of mankind.

ANUS. The posterior opening of the digestive tract.

APPENDAGE. Any limb or peripheral part of the body that diverges from the principal axis; specifically, the limbs of arthropods and vertebrates.

AQUATIC. Pertaining to water; living in water.

ARCHENTERON. The gastrula cavity.

ARREST. Suspension of a movement or process.

ARTERY. A blood vessel carrying blood from the heart to capillaries. *Cf.* **VEIN.**

ARTHRO-. Combining form, meaning "joint."

ARTIFACT. A natural object modified by man, such as a stone implement.

ARTIFICIAL PARTHENOGENESIS. *See* **PARTHENOGENESIS.**

ASEXUAL. Not sexual or not produced by sexual processes.

ASEXUAL REPRODUCTION. Reproduction without formation and union of gametes. *Cf.* **SEXUAL REPRODUCTION.**

ASSIMILATION. The taking up by the cells of useful substances brought to them by the circulating fluids, and the utilization of these substances in metabolism. *Cf.* **ANABOLISM.**

ASYMMETRY. Absence of symmetry.

ASYMPTOTE. A line that approaches nearer to some curve than any assignable distance, but, though infinitely extended, would never meet it. Characteristic of the logistic curve describing the growth of populations of organisms.

ATRIUM (*pl.* **ATRIA**). A membranous sac which serves as a passageway, such as the atrium (auricle) of the heart and the genital atrium.

AUDITORY. Pertaining to hearing or to the organs related to hearing.

AURICLE. The external ear of mammals or something that resembles such a projection; more specifically, a thin-walled, laterally expanded part of the heart that receives blood from the veins.

AUTOSOMES. Chromosomes that occur in pairs of similar size and shape and in equal numbers in both males and females of a species; chromosomes other than the sex chromosomes. *Cf.* **SEX CHROMOSOMES.**

AUTOTROPHIC. *See* **HOLOPHYTIC.**

AXIAL. Pertaining to the central line, or axis, of any symmetrical body; for example, the axial skeleton of vertebrates is composed of the skull and vertebral column.

BACKBONE. The vertebral column.

BACK-CROSS. A cross between a hybrid of the F_1 or F_2 generations and either of the parent types; a back-cross with the recessive parent type is used to distinguish heterozygous and homozygous individuals showing the dominant characteristics in an F_2 generation.

BACTERIA (*sing.* **BACTERIUM**). Microscopic, colorless, unicellular plants without discrete nuclei.

BALEEN. "Whalebone"; the material making up the feeding filters of several kinds of whales. Cetaceans may be divided into the toothed whales and the whalebone whales.

BARRIER. Any obstruction that prevents migration.

BEHAVIOR. The total reactions of an organism to its external environment.

BI-. Combining form, meaning "two"; same as **DI-.**

BILATERAL SYMMETRY. The symmetry of right and left halves of the body.

BINOMIAL NOMENCLATURE. System of naming animals, introduced by Linnaeus, in which each kind of organism is given two names, that of the genus and that referred to as the specific or trivial name.

BIOGENESIS. The production of living things from living things, not from non-living things; opposed to abiogenesis, or spontaneous generation; includes both reproduction and organic evolution.

BIOLOGY. The science of living things, both plants and animals; derived from *bios*, meaning life.

BIOTIC. Conditions in an environment related to, or dependent on, the living organisms inhabiting the environment; usually implies contrast with the physicochemical conditions.

BIRADIAL SYMMETRY. A simple bilateral symmetry obviously derived from radial symmetry; sometimes termed radiobilateral symmetry.

BLASTODERM. The developing part of the egg of a fish, reptile, or bird in which partial cleavage occurs; it gives rise to both the embryo and the embryonic membranes.

BLASTODISK. That part of the egg of a fish, reptile, or bird in which the nucleus is located and in which cleavage will occur.

BLASTOPORE. The opening of the gastrula cavity (archenteron) which is surrounded by the lips of the blastopore, or the germ ring.

BLASTULA. A developing individual characterized by a monoblastic structure.

BLASTULA CAVITY. The cavity of the blastula; cleavage cavity, or blastocoel.

BODY CAVITY. Any extensive cavity lying between the wall of the digestive tract and the body wall. *See* **COELOM** and **PSEUDOCOEL.**

BODY PLAN. The fundamental plan of organization of tissues, cavities, organs, and organ systems in animals.

BRANCHIAL. Pertaining to branchiae, or gills.

BRANCHIATE. Having gills (branchiae) as organs of external gas exchange. *Cf.* **PULMONATE.**

BROOD POUCH. Any cavity, other than a part of the reproductive tract, in which eggs or young are received and retained during at least a part of the developmental period.

BUCCAL. Pertaining to the mouth.

BUDDING. A method of asexual reproduction by unequal cell division, as in unicellular organisms, or by repeated divisions of totipotent cells to form an outgrowth, as in the coelenterates.

CAECUM (*pl.* **CAECA**). A blind pouch attached to any part of a digestive tract.

CALCAREOUS. Containing lime; chalky.

CAPILLARY. One of the many minute, thin-walled blood vessels found in organs of the body; substances enter and leave the blood through the walls of such vessels.

CARDIAC. Pertaining to or situated near the heart.

CARNIVOROUS. Feeding upon animals. *Cf.* **HERBIVOROUS** and **OMNIVOROUS.**

CASTE. Any one of the distinct forms of one species found among the social insects, such as the termites.

CATABOLISM. Collective term for energy-yielding reactions of cellular metabolism. *Cf.* **ANABOLISM.**

CAUDAL. Pertaining to or situated toward the tail.

CAUSE. The set of conditions as a result of which something occurs; frequently used for what is considered to be the most important of these conditions.

CELL. A mass of protoplasm containing one or more nuclei at some stage in its differentiation; the unit of structure and function in animals and plants.

CELL DIFFERENTIATION. The formation of tissue cells and gametes during histogenesis and gametogenesis, respectively; characterized by changes in the cytosome, or in the nucleus, or in both.

CELL DIVISION. The method of origin of new cells from pre-existing ones.

CELL LOCALIZATION. The bringing of groups of cells into definite positional relationships with other cell groups; brought about by cell movements.

CELL PRODUCTS. Non-cellular materials built up within cells and passing out of cells.

CELL SPECIALIZATION. The formation of different kinds of somatic cells associated with a physiological division of labor during the evolution of organisms; sometimes used to mean cell differentiation.

CELLULAR. Consisting of or pertaining to cells.

CELLULAR RESPIRATION. General term covering the utilization of oxygen in cellular metabolism. *Cf.* **METABOLISM, CATABOLISM,** and **RESPIRATION.**

CENTIMETER. The hundredth part of a meter; 1 inch equals 2.54 centimeters.

CEPHALIC. Pertaining to or situated toward the head.

CEPHALIZATION. The localization of important parts, such as the sense organs and the central nervous system, toward or in the head region during evolution.

CEPHALOTHORAX. A body division formed by the fusion of the head and the thorax in some of the arthropods.

CHEMICAL COORDINATION. Coordination brought about by the reaction of cells to the stimuli produced by endocrines that circulate in the blood. *Cf.* **COORDINATION** and **NERVOUS COORDINATION.**

CHEMORECEPTOR. A receptor sensitive to chemical compounds in solution.

CHITIN. The chemical compound characteristic of the exoskeletons of arthropods.

CHLORAGOGUE LAYER. Outer layer of the stomach-intestine of the earthworm and some other annelids, consisting of the highly modified visceral peritoneum.

CHLOROPHYLL. The green coloring matter of green plants, occurring also in plant-like flagellate protozoans.

CHLOROPLAST. An intracellular pigment body, characteristic of plant-like flagellate protozoans, containing the green pigment chlorophyll. *Cf.* **CHROMATOPHORES.**

CHROMATID. A half-chromosome; one of the four half-chromosomes forming a tetrad.

CHROMATIN. The readily stainable substance of the nucleus, most conspicuous during mitosis.

CHROMATOPHORES. Pigment-bearing cells, frequently capable of changes in shape and responsible for the color changes in animals like the chameleon and the squid.

CHROMOSOMAL ABERRATION. Any loss or gain of a part of a particular chromosome, of a whole chromosome, or of a haploid set of chromosomes; may give rise to a heritable variation.

CHROMOSOME. A mass of chromatin, of characteristic size and shape, visible in the nucleus at the time of mitosis; composed of a matrix containing at least two genonemata.

CILIA (*sing.* **CILIUM**). Short, hair-like protoplasmic extensions from the free surfaces of certain cells; capable of vibration and usually numerous. *Cf.* **FLAGELLUM.**

CIRCULATING FLUIDS. Blood and lymph.

CIRRUS (*pl.* **CIRRI**). A slender extension, occurring singly or in groups and frequently curved; a name used for many structures of diverse functions.

CLASS. A subdivision of a phylum; a group of next higher rank than an order.

CLASSIFICATION. The grouping together of organisms that have certain structural features in common.

CLEAVAGE. Cell division during the early period of development.

CLEAVAGE CAVITY. *See* **BLASTULA CAVITY.**

CLOACA. A common chamber through which egested and certain excreted materials, as well as the germ cells, leave the bodies of many vertebrates; analogous regions in some invertebrates.

CM. Abbreviation for centimeter.

COELOM (*pl.* **COELOMATA**). The body cavity of eucoelomate Metazoa, formed in and surrounded by mesodermal tissues; having a continuous peritoneal lining and a characteristic relationship to reproductive organs and nephridia. May be continuous or divided into chambers by partitions. *Cf.* **BODY CAVITY, HEMOCOEL, PSEUDOCOEL.**

COLONY. A group of individuals, unicellular or multicellular and of the same species, that have arisen from a common parent cell and remain attached or held together; also, insect societies.

COMMENSALISM. A form of symbiosis consisting of an association of two or more individuals, of different species, of which neither is parasitic but in which some benefit of the association may accrue to one rather than to both of the members. *Cf.* **MUTUALISM** and **PARASITISM.**

COMMISSURE. A connection between two ganglia of a pair, or right and left parts of the nervous system. *Cf.* **CONNECTIVE.**

COMMON CARRIER. A circulating fluid which transports numerous substances to and from the various parts of the body.

COMMON CENTER OF ORIGIN. A place in which the ancestors of different but related kinds of animals lived and from which they migrated over all possible routes as evolution occurred.

COMMUNITY. Collective term for all the organisms living in a particular general environment, interacting with each other and with the conditions characteristic of the environment.

COMPETITION. Relationship existing between two or more different organisms, or different kinds of organisms, both or all of which depend for their lives on certain foods, or substances, or space, available in their environment in only limited amounts. One of the bases for the "struggle for existence" between organisms in an environment.

CONDITION. To be a prerequisite of some event.

CONDITIONED REFLEX. A reflex action in which the reaction to a stimulus has been established by training or experimentation.

CONJUGATION. Temporary union of two cells during which exchange of nuclear materials occurs, as in *Paramecium*. *Cf.* **FERTILIZATION.**

CONNECTIVE. A longitudinal nerve cord extending between ganglia in different regions of the body. *Cf.* **COMMISSURE.**

CONSTITUENT. That which is a necessary part.

COORDINATION. The working together of different parts of an organism in such a way that it is physiologically balanced. *Cf.* **CHEMICAL COORDINATION** and **NERVOUS COORDINATION.**

COPULATION. *See* **SEXUAL UNION.**

CORTEX (*pl.* **CORTICES**). An outer or superficial layer.

CRANIAL. Pertaining to the skull.

CROSS-FERTILIZATION. Union of gametes produced by different individuals. *Cf.* **SELF-FERTILIZATION.**

CUTICLE. A non-cellular organic layer secreted by the cells of the outer surface of the body.

CYST. A protective capsule.

CYTOLOGY. The science of the structure of cells.

CYTOPLASM. The contents of the cytosome.

CYTOPLASMIC INCLUSIONS. Microscopic structures found in the cytoplasm, such as mitochondria and yolk spheres.

CYTOPYGE. Cell "anus" through which fecal material is egested by some protozoans.

CYTOSOME. The part of the cell surrounding the nucleus and limited by the cell membrane.

CYTOSTOME. Cell "mouth" through which food is ingested by some protozoans.

DATA (*sing.* **DATUM**). Observed and recorded facts.

DERMAL. Pertaining to the skin or outer covering of the body.

DERMIS. The inner layer of the skin, composed of connective tissue.

DETERMINERS. *See* **GENES.**

DEVELOPMENT. The transformation of a zygote into a multicellular organism; the consecutive processes of cell division, cell localization, and cell differentiation following syngamy.

DI-. Combining form, meaning "two"; same as **BI-.**

DIAPHRAGM. A partition; specifically, the partition forming the anterior boundary of the peritoneal cavity in mammals.

DIFFERENTIATION. *See* **CELL DIFFERENTIATION.**

DIFFUSE. To spread, as a fluid; to mix with another substance.

DIGAMETIC SEX. The sex of individuals that produce two classes of gametes which differ with respect to the presence of an X-chromosome; in most animals, the male sex.

DIGESTION. The chemical disintegration of food which precedes its absorption and utilization.

DIGESTIVE. Pertaining to digestion.

DIOECIOUS. Having sexually differentiated individuals; having the male and female gonads in separate individuals. *Cf.* **MONOECIOUS.**

DIPLOBLASTIC. Having only two germ layers, the ectoderm and endoderm, and a single cavity which has one external opening and is lined with endoderm. *Cf.* **MONOBLASTIC** and **TRIPLOBLASTIC.**

DIPLOID. Having two sets of chromosomes forming homologous pairs, as in somatic cells, primordial germ cells, and zygotes. *Cf.* **HAPLOID.**

DIRECT CELL DIVISION. *See* **AMITOSIS.**

DISCHARGE. The passage of a nerve impulse from a nerve fiber to an effector.

DISJUNCTION. The separation of the chromosomes of a homologous pair and their distribution into separate cells during one of the meiotic divisions. *Cf.* **SEGREGATION.**

DISTAL. Situated away from the center or place of attachment. *Cf.* **PROXIMAL.**

DIURNAL. Pertaining to the daytime; daily. *Cf.* **NOCTURNAL.**

DOMESTICATION. The taming or rearing of wild animals by man, with the consequent changes in their environments and habits of life.

DOMINANCE. The differentiation of a region under the influence of one gene, called the dominant gene, although an allelomorph, called the recessive gene, may be present; where dominance occurs, a heterozygous individual, with a single dominant gene, looks like a homozygous individual with two dominant genes but does not breed true.

DORSAL. Pertaining to or situated near the back or upper surface of an animal or part. *Cf.* **VENTRAL.**

DUCT. A tube, or canal, by which a liquid is conducted; usually restricted to such a tube that opens on a surface. *Cf.* **VESSEL.**

DUCTLESS GLAND. *See* **ENDOCRINE GLAND.**

DUCTUS (*pl.* **DUCTUS**). *See* **DUCT.**

ECOLOGICAL SUCCESSION. The orderly temporal sequence of forms succeeding each other in an environment undergoing gradual changes in its general conditions. As each environmental condition changes, forms previously adapted to existence in the environment either die out or emigrate, to be replaced by other organisms adapted to the new conditions.

ECOLOGY. The science of the relations of organisms to their external environment.

ECTODERM. The outermost of the two germ layers formed during gastrulation; covers the gastrula. *Cf.* **ENDODERM** and **MESODERM.**

ECTOPARASITE. A parasite that lives on the outside of its host. *Cf.* **ENDOPARASITE.**

ECTOPLASM. The outermost layer of the cell contents in Protozoa.

ECTOTHERMOUS. Animals having no capacity, or at most a very limited capacity, of maintaining their own body temperatures constant in the face of changes in the environmental temperature; loosely, "cold-blooded."

EFFECTOR. A region where a reaction occurs as a result of a stimulus; muscles and glands are effectors.

EFFERENT. Carrying away from a given region. *Cf.* **AFFERENT.**

EGESTION. The elimination of indigestible or undigested material from a place of digestion. *Cf.* **INGESTION.**

EGG AXIS. An imaginary line passing through the center of the egg and the point where the first polar body is formed; connects the animal pole of the egg with the vegetal pole.

EMBRYO. A young organism before its hatching or birth and before it is self-sustaining. *Cf.* **LARVA** and **JUVENILE.**

EMBRYOLOGY. The science of development.

EMBRYONIC CELL. *See* **TOTIPOTENT CELL.**

EMBRYONIC MEMBRANES. Cellular membranes formed in association with the embryo during development and related to its metabolic requirements; specifically, the yolk sac, amnion, chorion, and allantois in vertebrates.

ENCYST. To become enclosed in a cyst.

ENCYSTMENT. Process of encasement within a cyst. *Cf.* **EXCYSTMENT.**

ENDOCRINE. A secretion produced by an endocrine or ductless gland and serving as a stimulus in chemical coordination; sometimes called a hormone.

ENDOCRINE GLAND. A gland without a duct, the secretion of which passes into the blood stream.

ENDOCRINOLOGY. The science of the endocrines.

ENDODERM. The innermost of the two germ layers formed during gastrulation; forms the wall of the archenteron; sometimes called entoderm. *Cf.* **ECTODERM** and **MESODERM.**

ENDOMIXIS. A reproductive or pre-reproductive process characteristic of some ciliates, such as *Paramecium;* apparently somewhat analogous to the process of **CONJUGATION** but differs in that the changes involve only a single individual.

ENDOPARASITE. A parasite that lives within its host. *Cf.* **ECTOPARASITE.**

ENDOPLASM. The interior cytoplasm of a protozoan or of any other cell.

ENDOSKELETON. An internal skeleton; a cellular supporting structure formed from mesoderm. *Cf.* **EXOSKELETON** and **SKELETON.**

ENDOTHERMOUS. Animals possessing the capacity of maintaining a constant, or nearly constant, body temperature in the face of marked changes in the temperature of their environment; loosely, "warm-blooded."

ENERGY. See **TRANSFORMATION OF ENERGY.**

ENTEROCOEL. A true coelom formed primitively by the expansion into the blastocoel of hollow evaginations from the wall of the archenteron, or by a process evidently derived from such a type of development. *Cf.* **SCHIZOCOEL.**

ENTERON. A digestive cavity or tube lined by a cellular layer, the gastrodermis, of endodermal origin.

ENTODERM. Variant spelling of **ENDODERM.**

ENTOMOLOGIST. A student of the insects.

ENVIRONMENT. The total of surrounding conditions, usually with reference to the organism as a whole; in this sense, the external environment, as contrasted with the internal environment, or immediate surroundings of a part of an organism.

ENZYME. An organic catalyst, or substance that affects the rate of a chemical reaction but does not appear as one of its end products; there are many kinds of enzymes, and they are produced by all cells.

EPIDERMIS. The outer cellular layer of the body; the outer layer of the skin, an epithelium of ectodermal origin.

EQUILIBRIUM. The state of being balanced.

ERYTHROCYTE. A red blood cell. *Cf.* **LEUCOCYTE** and **LYMPHOCYTE.**

EUCOELOMATE. A metazoan possessing a true coelom. *See* **COELOM.**

EUGENICS. The science that applies the principles of genetics for the purpose of human betterment.

EUGLENOID. Pertaining to or resembling the euglena.

EVAGINATION. The movement of a group or layer of cells away from a cavity. *Cf.* **INVAGINATION.**

EVIDENCE. Facts related to some particular event.

EVOLUTION. The process of natural, consecutive change. *Cf.* **ORGANIC EVOLUTION.**

EXCRETA (sometimes **EXCRETIONS**). Waste products of metabolism, to be eliminated from the body.

EXCRETION. The process of elimination of the metabolic wastes.

EXCRETORY. Pertaining to the elimination of metabolic waste products.

EXCRETORY TUBULE. Any small duct that conveys nitrogenous waste products, such as the kidney tubules of vertebrates, the Malpighian tubules of insects, and the nephridia.

EXCURRENT. Affording an exit; leading outward. *Cf.* **INCURRENT.**

EXCYSTMENT. Emergence from a cyst. *Cf.* **ENCYSTMENT.**

EXOSKELETON. An external skeleton; a non-cellular, non-living structure, lying at the surface of the body, produced by the epidermis. *Cf.* **ENDOSKELETON** and **SKELETON.**

EXPERIMENTAL BREEDING. Breeding in such a way that the method of inheritance of given characters can be determined. *See* **HYBRIDIZATION.**

EXPERIMENTAL EMBRYOLOGY. The study of development by altering any one of the conditions affecting its course, such as the external environment.

EXTERNAL RESPIRATORY EXCHANGE (sometimes **EXTERNAL RESPIRATION**). *See* **GAS EXCHANGE.**

EXTRA-. Combining form, meaning "outside."

F_1 GENERATION. *See* **FIRST FILIAL GENERATION.**

F_2 GENERATION. *See* **SECOND FILIAL GENERATION.**

FACT. A real state of things as distinguished from a belief.

FACTORS. *See* **GENES.**

FACULTATIVE. Refers to organisms capable of a variety of different processes relating to a common function; for example, some bees, wasps, and other hymenopterans are capable of developing either with or without fertilization of the eggs, and this is spoken of as a case of **facultative parthenogenesis.** *Cf.* **OBLIGATE.**

FALSE COELOM. *See* **PSEUDOCOEL.**

FAMILY. A subdivision of an order; a group of next higher rank than a genus.

FATTY ACIDS. A group of organic acids formed by oxidation of alcohols.

FAULT. Geological term referring to discontinuities in strata of rock, resulting from breakage of the layers after they have buckled under lateral stresses.

FAUNA. The total of the animal life of a given region or period of time.

FEMALE GAMETE. *See* **OVUM.**

FERTILIZATION. The union of two gametes to form a single cell, the zygote; a complex process consisting of an initial activation of the ovum, followed by amphimixis. *See* **SYNGAMY;** *Cf.* **CONJUGATION.**

FIN. An extension from the body of an aquatic animal, used in locomotion.

FIRST FILIAL GENERATION. The individuals arising directly from a given mating; the F_1 generation. *See* **SECOND FILIAL GENERATION.**

FISSION. The division of an organism into two or more parts, each of which usually develops into a new individual; a method of asexual reproduction.

FLAGELLATE. Having one or more flagella.

FLAGELLUM (*pl.* **FLAGELLA**). A long, whip-like extension from the free surface of a cell, capable of vibration; the locomotor organelle of flagellate protozoans and of most metazoan spermatozoa. *Cf.* **CILIA.**

FLUCTUATION. A modification of a character that is conditioned by some change in the environment during development; a non-heritable variation. *Cf.* **MUTATION.**

FOLLICLE. A cellular sac or envelope.

FOOD. The material necessary for normal metabolism, that is, for cellular maintenance and growth and the synthesis of secretions. The source of energy for holozoic organisms.

FOOD CHAIN. A series of organisms in a community dependent on each other for food supplies; each "link" in the chain feeds upon the organism just below it and in turn serves as food for the one just above it. Different food chains in a community interact to form what are spoken of as "food webs."

FOSSIL. Anything of organic origin which was buried beneath the surface of the earth by natural causes in prehistoric times.

FRATERNAL TWINS. Two individuals, not necessarily of the same sex, that arise simultaneously from two zygotes in an animal which usually produces only one young at a time. *Cf.* **IDENTICAL TWINS.**

FREE-LIVING. Not sessile or parasitic; capable of actively obtaining its own food.

FUNGUS (*pl.* **FUNGI;** *adj.* **FUNGOUS**). A colorless plant of relatively simple organization.

GAMETE. A differentiated germ cell, usually ovum or spermatozoon. *Cf.* **SOMATIC CELL.**

GAMETOCYTE. A cell capable of differentiating into a gamete.

GAMETOGENESIS. The differentiation of gametes. *Cf.* **HISTOGENESIS.**

GANGLION. A mass of nerve cell bodies.

GAS EXCHANGE. The exchange of respiratory gases (oxygen and carbon dioxide) between the animal and its environment, either generally over the surface of the body or in specialized organs such as gills or lungs.

GASTRIC. Pertaining to the stomach.

GASTRULA. A developing individual characterized by a diploblastic structure.

GASTRULA CAVITY. The cavity of the gastrula, lined with endoderm and opening by way of the blastopore; the archenteron or gastrocoel.

GASTRULATION. The formation of a gastrula from a blastula by cell localization.

GEL. A semisolid or jelly-like state of protoplasm or any colloid. *Cf.* **SOL.**

GEMMULE. A reproductive body resistant to unfavorable environmental conditions, capable of germinating to produce a new individual; characteristic of many sponges. The **statoblasts** of fresh-water Ectoprocta are analogous formations.

GENE COMPLEX. All the genes present in a zygote.

GENE STRING. A linear series of genes constituting a linkage group.

GENERIC. Pertaining to a genus.

GENES. The units of inheritance, transmitted from one generation to the next by way of the gametes and conditioning the appearance of an individual's characters during its development.

GENETICIST. A student of heredity and variation; more specifically, a student of experimental breeding.

GENETICS. The science of heredity and variation.

GENITAL. Pertaining to the organs of reproduction.

GENONEMATA (*sing.* **GENONEMA**). Slender threads of chromatin which can be distinguished within the chromosomes during mitosis, and sometimes in the nucleus between periods of division.

GENUS (*pl.* **GENERA**). One of the subdivisions of a family; a group of next higher rank than a species.

GERM CELL. A cell, in a multicellular organism, that is capable of reproduction by syngamy. *Cf.* **SOMATIC CELL** and **GAMETE.**

GERM LAYERS. The cell layers resulting from the early cell localizations during the establishment of the body plan in development; specifically, ectoderm, endoderm, and mesoderm. *Cf.* **DIPLOBLASTIC** and **TRIPLOBLASTIC.**

GILL. An organ of external respiratory exchange in branchiate aquatic animals.

GILL SLIT. A pharyngeal cleft; one of the paired openings that appear in the region of the pharynx during the development of hemichords and chordates, and along the sides of which gills develop in the aquatic chordates.

GLAND. One or more cells differentiated for the production of some secretion.

GONAD. An organ in which gametes are differentiated; an ovary or testis.

GONODUCT. A duct through which gametes or embryos pass out of an animal.

GONOPORE. External opening of a reproductive duct.

GROWTH. An increase in the size of an organism that results when anabolic processes occur at a more rapid rate than catabolic processes.

GROWTH PERIOD. The period of gametogenesis that immediately precedes the meiotic divisions.

GUSTATORY. Pertaining to tasting.

GUT. The digestive tract.

HABITAT. The area or region in which an organism lives; the environmental conditions under which a species can exist.

HAPLOID. Having a single set of chromosomes that do not occur in pairs. Gametes are haploid cells. *Cf.* **DIPLOID.**

HEAD. The front end of an animal, or part, if it is distinguished from the rest in any way.

HEART. A pulsating organ of the blood-vascular system; a blood vessel modified for propelling the blood.

HEMOCOEL. A body cavity, which may be a pseudocoel or may develop in part from a true coelom, containing a fluid that may be called blood or lymph and functioning as part of the circulatory system.

HEMOGLOBIN. The pigment of the blood with which oxygen combines to form oxyhemoglobin.

HEPATIC. Pertaining to the liver.

HERBIVOROUS. Feeding upon plants. *Cf.* **CARNIVOROUS** and **OMNIVOROUS.**

HEREDITARY DETERMINERS. *See* **GENES.**

HEREDITARY UNITS. *See* **GENES.**

HEREDITY. The resemblance of successive generations of individuals, conditioned by the transmission of genes during reproduction.

HERITABLE VARIATION. A modification in either structure or function that recurs in successive generations; a variation conditioned by changes in a gene or in a gene complex. *Cf.* **MUTATION, CHROMOSOMAL ABERRATION,** and **FLUCTUATION.**

HERMAPHRODITIC. Possessing both male and female gonads; monoecious.

HETEROZYGOTE. A zygote formed by the union of two gametes that differ with respect to particular genes. *Cf.* **HOMOZYGOTE.**

HETEROZYGOUS. Developing from a heterozygote. *Cf.* **HOMOZYGOUS.**

HIBERNATION. A cessation of activity by an animal during cold weather.

HISTOGENESIS. The differentiation of tissue cells. *Cf.* **GAMETOGENESIS.**

HISTOLOGY. The science of the structure of animals as revealed by the microscope; the study of cells as they are grouped to form tissues and organs. *Cf.* **ANATOMY.**

HOLOPHYTIC. A form of nutrition characteristic of green plants and of chlorophyll-bearing plant-like protozoans. It involves the photosynthetic formation of carbohydrates from carbon dioxide and water. *Cf.* **SAPROZOIC** and **HOLOZOIC.**

HOLOZOIC. A form of nutrition in which foods are ingested in solid or particulate form. *Cf.* **HOLOPHYTIC** and **SAPROZOIC.**

HOMOLOGOUS CHROMOSOMES. A pair of chromosomes similar in size and shape, one of which is contributed by each of the gametes that unite to form the zygote.

HOMOLOGY (*adj.* **HOMOLOGOUS**). Correspondence in fundamental structure or in embryonic and presumably phylogenetic origin. *Cf.* **ANALOGY.**

HOMOZYGOTE. A zygote formed by the union of two gametes that are alike with respect to particular genes. *Cf.* **HETEROZYGOTE.**

HOMOZYGOUS. Developing from a homozygote. *Cf.* **HETEROZYGOUS.**

HORMONE. *See* **ENDOCRINE.**

HOST. An organism that nourishes a parasite.

HYBRID. An individual whose parents differed with respect to one or more characters. *Cf.* **HYBRIDIZATION.**

HYBRIDIZATION. The breeding of individuals that differ with respect to one or more characters. *See* **EXPERIMENTAL BREEDING.**

HYPER-. Combining form, meaning "over," either in position or degree. *Cf.* **HYPO-** and **SUPER-.**

HYPO-. Combining form, meaning "under," either in position or degree. *Cf.* **HYPER-.**

HYPOTHESIS. A tentative correlation or explanation of observed facts which is usually stated as an aid to further study of related facts; if supported by additional data, a hypothesis may become a theory.

IDENTICAL TWINS. Two individuals, always of the same sex, which arise during development from a single zygote. *Cf.* **FRATERNAL TWINS.**

IMAGO. Adult stage of an insect.

IMPULSE. *See* **NERVE IMPULSE.**

INCURRENT. Affording an entrance; leading inward. *Cf.* **EXCURRENT.**

INDEPENDENT EFFECTOR. A cell responding directly to changes in its environment; an effector that is independent of a reflex arc.

INDIRECT CELL DIVISION. *See* **MITOSIS.**

INDIVIDUAL. A physiologically balanced, living unit; an animal or plant.

INGESTION. The act of taking food into a place of digestion. *Cf.* **EGESTION.**

INSTINCT. Reflex action, frequently of a very complex character, dependent on an inherited reflex arc.

INTEGUMENT. The outer covering of the body; the skin or a derivative of it.

INTELLIGENCE. The capacity to profit by experience, based on analysis and association of ideas.

INTER-. Combining form, meaning "between" or "among."

INTERNAL PARASITE. *See* **ENDOPARASITE.**

INTERNAL SECRETION. *See* **ENDOCRINE.**

INTRA-. Combining form, meaning "within."

INVAGINATION. The movement of a group or layer of cells into a cavity. *Cf.* **EVAGINATION.**

INVERTEBRATE. An animal without a vertebral column or backbone. *Cf.* **VERTEBRATE.**

ISOGAMETES. Gametes of equal size. *Cf.* **ANISOGAMETES.**

ISOGAMY. Fusion of gametes of equal size. *Cf.* **ANISOGAMY** and **FERTILIZATION.**

ISOLECITHAL EGG. An egg in which the yolk is not abundant and is almost uniformly distributed throughout the cytosome. *Cf.* **TELOLECITHAL EGG.**

JUVENILE. A self-sustaining young organism that is like the adult of the species except in size and reproductive maturity. *Cf.* **EMBRYO** and **LARVA.**

KINETOSOME. The basal body of a cilium; apparently the part of the ciliary mechanism responsible for initiation of ciliary beating, and in ciliate protozoans possessing important morphogenetic capacities.

LACUNA (*pl.* **LACUNAE**). A cavity or space.

LAND BRIDGE. A land connection between two other land regions; most often used for such a connection that has been submerged.

LARVA (*pl.* **LARVAE**). A self-sustaining young organism that does not resemble the adult. *Cf.* **EMBRYO** and **JUVENILE.**

LETHAL. Capable of bringing about death.

LEUCOCYTE. A granular white blood cell; a non-pigmented or colorless blood cell. *Cf.* **LYMPHOCYTE** and **ERYTHROCYTE.**

LIFE CYCLE. The history of an organism or species with reference to its methods of reproduction and development.

LINEAR. Like a line or thread.

LINKAGE. The occurrence of certain characters together in successive generations of individuals; a condition arising from the transmission of genes in linkage groups.

LINKAGE GROUP. A group of genes that is transmitted from one generation to the next as a unit. *Cf.* **GENE STRING.**

LOCUS (*pl.* **LOCI**). A place; a locality; the position occupied by a gene on a gene string.

LOPHOPHORE. A variously-shaped, tentacle-bearing feeding organ surrounding or lying near the mouth, in such forms as Ectoprocta, Brachiopoda, and Phoronidea.

LUMEN (*pl.* **LUMINA**). A passageway or cavity.

LUMINESCENCE. The emission of light arising from chemical reactions within cells.

LYMPH. A circulating fluid consisting of plasma and white blood cells.

LYMPH GLAND. An organ in which lymphocytes are differentiated.

LYMPHATIC. A vessel that transports lymph.

LYMPHOCYTE. A non-granular white blood cell; a non-pigmented or colorless blood cell. *Cf.* **LEUCOCYTE** and **ERYTHROCYTE.**

M. Abbreviation for meter.

MACRO-. Combining form, meaning "large." *Cf.* **MICRO-.**

MALE GAMETE. *See* **SPERMATOZOON.**

MALNUTRITION. A condition resulting from any deficiency in nourishment.

MAMMARY GLANDS. Glands that secrete milk; characteristic of mammals.

MANDIBULATE. Possessing jaws, or mandibles, and thus able to bite.

MATRIX (*pl.* **MATRICES**). That which encloses anything; the intercellular material of some sustentative tissues; the part of a chromosome surrounding the genonemata.

MATURATION. The process of maturing or differentiation of the germ cells. *See* **GAMETOGENESIS.**

MEIOSIS. The process by which the number of chromosomes is changed from the diploid to the haploid number; brought about by two nuclear divisions following the growth period during gametogenesis. *Cf.* **MITOSIS.**

MEROGONY. A form of asexual reproduction involving multiple fission, characteristic of the so-called merozoite stages of some sporozoan parasites. Often referred to as schizogony.

MESENCHYME. Loosely arranged cells of irregular shape which are relatively undifferentiated and give rise to different tissues; of mesodermal origin.

MESENTERY. A double layer of cells connecting the visceral and parietal peritoneum and serving as a support for the coelomic organs.

MESO-. Combining form, meaning "middle."

MESOBLAST. One of two cells in schizocoelous eucoelomate animals, from which proliferate the masses or rods of mesoderm cells later hollowed out to form the coelomic pouches.

MESODERM. The germ layer that is localized between the ectoderm and endoderm.

MESODERMAL SOMITES. Compact, similar groups of mesodermal cells lying along each side of the neural tube.

MESORCHIUM (*pl.* **MESORCHIA**). The mesentery supporting a testis.

MESOVARIUM (*pl.* **MESOVARIA**). The mesentery supporting an ovary.

META-. Combining form, meaning behind or beyond in position, or later in time.

METABOLIC CELL. A cell that is not in the process of division; sometimes called a resting cell.

METABOLISM. The fundamental manifestation of life in cells; a collective term for the chemical reactions in cells. *Cf.* **ANABOLISM** and **CATABOLISM.**

METAGENESIS. A type of life cycle in which a sexually reproducing organism arises from and gives rise to an asexually reproducing organism.

METAMERE. *See* **SOMITE.**

METAMERISM. The condition of being divided into a number of similar parts, arranged in linear series and called metameres or somites.

METAMORPHOSIS. The alteration of structure that an animal undergoes after it hatches; specifically, the transformation of a larva into an adult.

METAZOA (*sing.* **METAZOON** or **METAZOAN**). Multicellular animals. *Cf.* **PROTOZOA.**

METER. A measure of length equal to 39.37 inches.

MICRO-. Combining form, meaning "small." *Cf.* **MACRO-.**

MICRON. Unit of measurement in microscopy; 0.001 millimeter.

MIGRATION. A movement of animals into a new locality, usually in search of food.

MILLIMETER. The thousandth part of a meter; the tenth part of a centimeter; 1 inch equals 25.4 millimeters.

MISSING LINK. *See* **SYNTHETIC TYPE.**

MITOSIS. The process of indirect nuclear division during which chromosomes appear and duplicate longitudinally, the two members of each sister pair passing into separate nuclei; cells arising after mitosis contain the diploid number of chromosomes. *Cf.* **AMITOSIS** and **MEIOSIS.**

MM. Abbreviation for millimeter.

MOLT. To shed an exoskeleton or any integumentary structure.

MONOBLASTIC. Having a closed cavity surrounded by a single layer of cells. *Cf.* **DIPLOBLASTIC** and **TRIPLOBLASTIC.**

MONOECIOUS. A condition, normal in many animals, in which reproductive organs characteristic of both sexes are present and functional in each individual; hermaphroditic. *Cf.* **DIOECIOUS.**

MORPHOLOGY. The science of structure.

MOTORIUM. The neuromotor center responsible for integration and coordination of the ciliary system in ciliate protozoans.

MOUTH. The opening of the digestive tract through which ingestion occurs.

MOUTH CAVITY. The part of the digestive tract into which food is first taken.

MOUTH PARTS. The appendages related to the mouth of an arthropod.

MUCOSA. The cellular lining of the digestive tract, derived from endoderm.

MUCUS (*adj.* **MUCOUS**). A sticky or slimy fluid secreted by certain glands, widespread among animals and used in a variety of functions such as lubrication, protection, etc.

MULTI-. Combining form, meaning "many." *Cf.* **UNI-.**

MUTATION. A modification of a character that is conditioned by some change in the gene complex; a heritable variation; specifically, an alteration of a gene. *Cf.* **FLUCTUATION.**

MUTUALISM. A form of symbiosis consisting of an association between two or more individuals, of different species, with benefit accruing to both members of the association; the term **symbiosis** is sometimes restricted to this situation. *Cf.* **COMMENSALISM** and **PARASITISM.**

NASAL. Pertaining to the nose or nostril.

NEPHRIDIUM (*pl.* **NEPHRIDIA**). An excretory tubule found in arthropods, mollusks, and some other animals.

NERVE. A bundle of nerve fibers lying outside the central nervous system.

NERVE CELL. *See* **NEURON.**

NERVE CORD. A compact cord composed of neurons and forming part of a central nervous system; it may or may not be ganglionated. *Cf.* **CONNECTIVE.**

NERVE FIBERS. Extensions of the cytosome of a neuron; dendrites and axons.

NERVE IMPULSE. A physicochemical disturbance established and conducted in a neuron as a result of a stimulus.

NERVE NET. The association of neurons to form a diffuse network without ganglionic aggregations; the only nervous system in some simple metazoans and a part of the peripheral nervous system in many more complex forms.

NERVE RING. A circular nerve cord.

NERVOUS COORDINATION. Coordination brought about by the reaction of parts to the discharge of nerve impulses. *Cf.* **COORDINATION** and **CHEMICAL COORDINATION.**

NEURAL. Pertaining to the nervous system.

NEURON. A nerve cell; a cell characterized by conspicuous extensions of the cytosome, known as dendrites and axons, over which nerve impulses pass.

NICHE. The specific position or function of a particular type of organism in an environment; comparable niches in different environments may be filled by a variety of different organisms.

NOCTURNAL. Pertaining to the night. *Cf.* **DIURNAL.**

NOTOCHORD. A cellular cord formed between the archenteron and the neural tube during the early development of all chordates; the vertebral column is formed around but not from the notochord in vertebrates.

NUCLEUS (*pl.* **NUCLEI**). The part of the cell containing chromatin and limited by the nuclear membrane.

NUTRITION. The science of foods; the basic processes or manner of obtaining foods.

NYMPH. An immature postembryonic stage in the life cycle of a paurometabolous insect.

OBLIGATE. Refers to conditions or processes required for the life of an organism; for example, an organism that cannot live in the presence of atmospheric oxygen is spoken of as an obligate anaerobe. *Cf.* **FACULTATIVE.**

OLFACTORY. Pertaining to the sense of olfaction, or smell.

OMNIVOROUS. Feeding upon both plants and animals. *Cf.* **CARNIVOROUS** and **HERBIVOROUS.**

ONTOGENETIC. Related to the origin and development of the individual. *Cf.* **PHYLOGENETIC.**

OÖGENESIS. The differentiation of the ova. *Cf.* **SPERMATOGENESIS.**

OPHTHALMIC. Pertaining to the eye.

OPTIC. Pertaining to vision or to the eye.

OPTIMUM. Conditions of temperature, salinity, pH, humidity or any other environmental factor under which an organism performs its vital functions with maximum efficiency.

ORAL. Pertaining to the mouth, or place of ingestion.

ORDER. One of the subdivisions of a class; a group of next higher rank than a family.

ORGAN. A group of tissues associated together for the performance of a special function. *Cf.* **SYSTEM.**

ORGANIC. Pertaining to organisms or resulting from their activities; in chemistry, compounds containing carbon.

ORGANIC EVOLUTION. The process of descent with modification as a result of which present-day species of animals have arisen from those of the past. *Cf.* **EVOLUTION.**

ORGANISM. An animal or plant.

ORGAN SYSTEM. *See* **SYSTEM.**

OSTIUM. An opening or entrance.

OVARY. A gonad in which ova undergo differentiation. *Cf.* **TESTIS.**

OVIPAROUS. Egg-laying; producing young that develop from eggs which hatch outside the body of the mother. *Cf.* **OVOVIVIPAROUS** and **VIVIPAROUS.**

OVOVIVIPAROUS. Producing young that develop from eggs which hatch within the body of the mother. *Cf.* **OVIPAROUS** and **VIVIPAROUS.**

OVULATION. The discharge of eggs from the ovary.

OVUM (*pl.* **OVA**). A mature or differentiated female germ cell; a macrogamete. *Cf.* **SPERMATOZOON.**

PALEONTOLOGY. The study of structure, probable interrelationships, and distribution of animals now extinct and known only through their fossil and other remains.

PALP. A feeler.

PAPILLA (*pl.* **PAPILLAE**). A rounded, thick process or extension.

PARAMYLUM. A starch-like carbohydrate synthesized and stored in many plant-like flagellate protozoans.

PARASITE. An organism that lives in or on another, at the expense of the latter. *Cf.* **HOST.**

PARASITISM. A form of symbiosis, consisting of an association between organisms of different species in which only one, the parasite, is benefited; the presence of the parasite is usually detrimental to its host. *Cf.* **COMMENSALISM, SYMBIOSIS,** and **MUTUALISM.**

PARENCHYMA. A loose, mesh-like tissue of irregularly shaped cells, of mesodermal origin, lying between the gut wall and the body wall in acoelomate animals.

PARIETAL. Pertaining to wall; specifically, to the lining of the coelom.

PARTHENOGENESIS. The development of an egg without union with a spermatozoon; may be natural or follow an artificial activation.

PEDAL. Pertaining to the foot.

PEDOGENESIS. Reproduction by individuals that are not adult.

PELAGIC. Living at or near the surface of the ocean at some distance from land.

PELLICLE. A delicate layer surrounding a cell, as in some Protozoa.

PENIS (*pl.* **PENES**). An organ functioning during sexual union and characteristic of the males of many species; of diverse structure and embryonic origins.

PERI-. Combining form, meaning "around" or "near."

PERICARDIAL. Surrounding the heart.

PERICARDIUM. The peritoneum of the pericardial cavity; also used for the pericardial cavity and its walls.

PERIPHERAL. Related to or situated on or toward the surface.

PERISTOME. Membranous area surrounding the mouth.

PERITONEUM. The compact cellular layer, usually squamous and of mesodermal origin, that forms the continuous lining of the body cavity in eucoelomate animals.

PHENOMENON (*pl.* **PHENOMENA**). A directly observed fact.

PHYLOGENETIC. Related to the origin and evolution of a species or other group of organisms. *Cf.* **ONTOGENETIC.**

PHYLUM (*pl.* **PHYLA**). One of the major subdivisions of the Animal and Plant Kingdoms.

PHYSIOLOGICAL BALANCE. Functional unity of a cell or organism, resulting either from lack of cell specialization or from well-developed coordination.

PHYSIOLOGY. The science of function.

PIGMENT. Organic coloring matter.

PLACENTA (*pl.* **PLACENTAE**). The organ by means of which the mammalian embryo is nourished during development; derived in part from the uterine wall and in part from embryonic membranes.

PLASMA. The liquid portion of the blood and lymph.

PLEURAL. Pertaining to the cavity surrounding the lungs or to the membrane lining such a cavity.

POLAR AXIS. An axis between two opposite poles. *Cf.* **POLARITY.**

POLAR BODY. A small, non-functional cell produced at each meiotic division in oogenesis; there will be three of these if the first polar body divides at the time of the second meiotic division.

POLARITY. A characteristic resulting from differentiation between the two ends of a cell or of an organism.

POLLINATE. To convey pollen, produced by male organs, to the female organs in plants.

POLOCYTES. The polar bodies.

POLY-. Combining form, meaning "many."

POLYEMBRYONY. The development of several embryos from one zygote.

POLYP. Any animal with many foot-like processes; specifically, one of the individuals of a coelenterate colony.

POPULATION. A group of individuals of the same species that do not have the same genetic constitution and consequently give rise to new combinations in successive generations; pure lines can be sorted out of a population by selection. *Cf.* **PURE LINE.**

POSTERIOR. Pertaining to or situated near the end away from the head; the hind part of an animal or part; opposite to anterior.

PREDATORY. Capturing other animals for food.

PREHENSILE. Fitted for grasping or holding.

PREHUMAN. Existing before the appearance of man upon the earth.

PRIMATE. A member of the order Primates, which includes all kinds of monkeys, the lemurs, and man.

PRIMORDIAL. First in order; primitive.

PRIMORDIUM (*pl.* **PRIMORDIA**). A beginning.

PROCTODEUM (*pl.* **PROCTODEA**). The ectodermal invagination which forms the most posterior part of the digestive tract during development. *Cf.* **STOMODEUM.**

PRONUCLEUS (*pl.* **PRONUCLEI**). The nucleus of a gamete; contains the haploid number of chromosomes.

PROPAGATION. The increase in numbers resulting from reproduction.

PROTONEPHRIDIUM. A flame bulb or solenocyte, in which a tuft of cilia or a single flagellum, respectively, creates currents in an intracellular duct system moving fluids from lymph spaces or a pseudocoel to the exterior. Classically interpreted as functioning in excretion, but may be involved rather in salt and water balance.

PROTOPLASM. The contents of living cells.

PROTOZOA (*sing.* **PROTOZOON** or **PROTOZOAN**). The phylum of the unicellular animals; unicellular animals. *Cf.* **METAZOA.**

PROTOZOOLOGY. The science of Protozoa.

PROTRACTOR MUSCLE. A muscle that extends a part or draws it forward. *Cf.* **RETRACTOR MUSCLE.**

PROXIMAL. Situated toward the center or place of attachment. *Cf.* **DISTAL.**

PSEUDOCOEL. A body cavity that lacks a continuous peritoneal lining and does not develop in mesoderm; may represent remnants of the blastocoel, and may be partially occupied by mesenchyme and structures of mesodermal origin. *Cf.* **COELOM.**

PSEUDOPODIUM (*pl.* **PSEUDOPODIA**). A temporary protrusion of a cell by means of which locomotion is effected or extracellular material engulfed.

PULMONARY. Pertaining to the lungs.

PULMONATE. Having lungs or lung-like structures as specialized organs of respiratory exchange. *Cf.* **BRANCHIATE.**

PURE LINE. A group of individuals of the same species that are homozygous for some particular character or characters and consequently breed true; variations in a pure line are usually fluctuations. *Cf.* **POPULATION.**

PYLORIC. Pertaining to the opening between the stomach and intestine.

PYRAMID OF NUMBERS. Concept derived from the numerical relationships existing between organisms in a community. In a food chain the basal herbivorous animals are extremely numerous; at each succeeding step in the chain, numbers become smaller, until the final type at the end of the chain is represented in the community by only a relatively few individuals.

RADIAL SYMMETRY. Symmetry in all planes passing through a longitudinal axis, as in a cylinder, or in which parts are arranged around an axis like the spokes of a wheel.

REASSOCIATION. The coming together of parts that previously have been artificially separated.

RECEPTION. The process that occurs in a receptor; the initial response to a stimulus.

RECEPTOR. A region especially sensitive to changes in the environment; may be a sensory cell or a complex sense organ containing many sensory cells.

RECESSIVE GENE. A gene that is without appreciable effect when associated with its dominant allelomorph. *Cf.* **DOMINANCE.**

RED BLOOD CELL. *See* **ERYTHROCYTE.**

REFLEX ACTION. An automatic response to a stimulus; the functional basis of nervous coordination.

REFLEX ARC. An afferent and efferent neuron, with or without interpolated adjustor neurons, so associated as to conduct impulses from a receptor to an effector; the functional basis of nervous coordination.

REGENERATION. The process of replacing a lost part.

RENAL. Pertaining to the kidney.

REPRODUCTION. The capacity as a result of which certain cells of an organism can become detached and, either alone or after union with cells of another organism of the same kind, give rise to a new individual capable of becoming like the parent or parents in all essential respects; the capacity upon which continuity of a species depends.

REPRODUCTIVE ORGAN. *See* **GONAD.**

RESEARCH. Continued search after facts and principles.

RESPIRATION. A general term which subsumes (1) external gas exchange between the organism and its environment; (2) transport of oxygen and carbon dioxide between the point of external exchange and the cells; and (3) the utilization of oxygen in cellular metabolism. *See* **GAS EXCHANGE, METABOLISM,** and **CELLULAR RESPIRATION.**

RESPIRATORY. Pertaining to respiration.

RESPIRATORY EXCHANGE. *See* **GAS EXCHANGE.**

RESPONSIVENESS. The capacity enabling living cells to respond to stimuli; the capacity responsible for coordination and behavior.

RETRACTOR MUSCLE. A muscle that withdraws a part or pulls it backward. *Cf.* **PROTRACTOR MUSCLE.**

RHABDITE. A rod-like structure produced in certain epidermal gland cells among free-living turbellarians; function unknown, but may be involved in adhesion to the substrate.

RUDIMENTARY. Embryonic; not completely developed; having no function; frequently but not correctly used to mean vestigial.

SAPROZOIC. A form of nutrition in which the organism requires external sources of organic nutrients which are not, however, ingested in particulate form but absorbed in solution through the body wall. *Cf.* **HOLOZOIC** and **HOLOPHYTIC.**

SCHEMATIC. Made or done according to a fundamental plan.

SCHIZOCOEL. A coelom formed through the development and enlargement of clefts or spaces within previously solid rods or blocks of mesodermal cells, proliferated from mesoblasts or pole cells. *Cf.* **ENTEROCOEL.**

SCIENCE. Knowledge gained by systematic observation, experimentation, and reasoning; factual information, correlated and systematized.

SECOND FILIAL GENERATION. The offspring from a mating of individuals of an F_1 generation; the F_2 generation.

SECRETION. Substance released from a cell, necessary for normal functions of the individual; also, the process of production and release of the substance.

SEDENTARY. Remaining in one place; not free-swimming, as a tube-dwelling animal. *Cf.* **SESSILE.**

SEGMENT. A part cut off or marked as separate from others; a natural division of the body or a part of it. *Cf.* **SOMITE.**

SEGREGATION. The separation of allelomorphic genes and their distribution into separate cells during one of the meiotic divisions. *Cf.* **DISJUNCTION.**

SELF-FERTILIZATION. Union of gametes produced by the same individual which may occur in some hermaphroditic organisms. *Cf.* **CROSS-FERTILIZATION.**

SEMINAL. Pertaining to or containing spermatozoa.

SEMINIFEROUS TUBES. Tubes of the testis along the walls of which the spermatozoa are differentiated.

SENSE ORGAN. A multicellular receptor; an organ containing cells especially sensitive to some particular type of stimulus.

SENSORY CELL. A unicellular receptor.

SEPTUM (*pl.* **SEPTA**). A partition between two cavities.

SEROLOGY. Study of blood serum; specifically, study of the immunity reactions developed by mammals and revealed by their sera; particularly useful in determining the apparent degrees of chemical interrelationship between the proteins of different kinds of animals.

SERUM. The liquid that separates from a blood clot; blood serum contains no cells or fibrin.

SESSILE. Attached; not free-swimming. *Cf.* **SEDENTARY.**

SETA (*pl.* **SETAE**). A bristle.

SEX. A characteristic condition of animals in which the individuals are either male or female and are distinguished essentially by the production of spermatozoa or ova, respectively.

SEX CHROMOSOMES. Chromosomes that differ in number and distribution in the males and females of a species; the X- and Y-chromosomes. *Cf.* **AUTOSOMES.**

SEX-LINKED INHERITANCE. The inheritance of characters conditioned by genes carried by the X-chromosomes.

SEX-REVERSAL. The loss of original sex characters and the assumption of those of the opposite sex.

SEXUAL REPRODUCTION. Reproduction by union of gametes like those produced by sexually differentiated individuals; this term is commonly used as a synonym for reproduction by syngamy. *Cf* **ASEXUAL REPRODUCTION.**

SEXUAL UNION. Temporary association of male and female organisms during which sperm are introduced into the reproductive tract of the female.

SILICEOUS. Containing or consisting of silica, which is characteristic of sand.

SINUS (*pl.* **SINUS** or **SINUSES**). A cavity.

SIPHON. A canal.

SKELETON. The hard parts of an organism which serve to support and protect soft parts. *Cf.* **ENDOSKELETON** and **EXOSKELETON.**

SOCIAL. Living in groups. *Cf.* **SOLITARY.**

SOL. A liquid state of protoplasm or any colloid. *Cf.* **GEL.**

SOLENOCYTE. *See* **PROTONEPHRIDIUM.**

SOLITARY. Living alone. *Cf.* **SOCIAL.**

SOMATIC. Pertaining to the body of an organism.

SOMATIC CELL. In colonial Protozoa, a cell that has lost the capacity of reproduction. In Metazoa, a cell which may divide in the growth of the organism but which is not directly involved in the reproductive activities of the individual. *Cf.* **GERM CELL.**

SOMITE. One of a series of homologous parts arranged in a row. *Cf.* **SEGMENT** and **MESODERMAL SOMITES.**

SPECIES (*pl.* **SPECIES**). A subdivision of a genus, sometimes separated into varieties.

SPERM. *See* **SPERMATOZOON.**

SPERMATOGENESIS. The differentiation of the spermatozoa. *Cf.* **OÖGENESIS,**

SPERMATOZOON (*pl.* **SPERMATOZOA**). A mature or differentiated male germ cell; a microgamete. *Cf.* **OVUM.**

SPERMIOGENESIS. The cytosomal differentiation of a spermatozoon; the transformation of a spermatid into a spermatozoon.

SPINAL. Pertaining to the vertebral column.

SPONGOCOEL. The characteristic major internal cavity of a sponge, either lined by choanocytes (as in the simplest sponges) or lined by endopinacocytes and receiving currents of water from radially disposed flagellated chambers.

SPORULATION. Reproduction by multiple fission.

STERNAL. Pertaining to the ventral midregion of arthropods; pertaining to the breastbone, or sternum, of vertebrates.

STIMULUS (*pl.* **STIMULI**). An effective change in the environment that provokes a response on the part of an organism.

STOMODEUM (*pl.* **STOMODEA**). The ectodermal invagination which forms the mouth cavity during development. *Cf.* **PROCTODEUM.**

STROBILIZATION. A method of reproduction by linear budding.

STRUCTURE. The arrangement or organization of parts of an organism.

SUB-. Combining form, meaning "under" or "below."

SUBSTRATUM (*pl.* **SUBSTRATA**). Anything which underlies or supports; a substrate.

SUPER-. Combining form, meaning "over"; same as **HYPER-;** opposite to **SUB-.**

SUPERFICIAL. Lying on or near the surface.

SUPRA-. Combining form, meaning "above"; same as **SUPER-.**

SYMBIOSIS. Any biotic situation in which two or more individuals of different species are mutually interdependent or otherwise closely related. *See* **PARASITISM, MUTUALISM,** and **COMMENSALISM.**

SYMMETRY. The reversed repetition of parts around an axis or on opposite sides of any plane, so that mirrored halves result from a separation along the axis or plane of symmetry.

SYNAPSE. The place of contact between two nerve fibers.

SYNAPSIS. The temporary pairing of homologous chromosomes which precedes the first meiotic division; occurs during the growth period.

SYNGAMY. *See* **FERTILIZATION.**

SYNTHESIS. The building-up of a chemical compound from simpler compounds or molecules.

SYNTHETIC TYPE. A species that represents an intermediate condition between well-recognized groups of organisms; a primitive ancestral type from which more highly specialized types have arisen.

SYSTEM. A group of structurally related organs which perform some general function.

TACTILE. Pertaining to the sense of touch.

TAXIS. *See* **TROPISM.**

TAXONOMY. The science of classification.

TELOLECITHAL EGG. An egg in which the yolk is abundant and concentrated in or toward the vegetal hemisphere. *Cf.* **ISOLECITHAL EGG.**

TENTACLE. An elongated, flexible, cellular process of the body.

TERRESTRIAL. Living on land.

TESTIS (*pl.* **TESTES**). A gonad in which spermatozoa undergo differentiation. *Cf.* **OVARY.**

THEORY. A conception of how something has been brought about; an explanation or correlation of observed facts; theories may be disproved, because they are the products of man's thinking.

THERMAL. Pertaining to heat.

THORAX (*pl.* **THORACES**). A part of the body between the head and abdomen.

TISSUE. A group of somatic cells differentiated in the same way for the performance of the same function.

TOTIPOTENT CELL. An undifferentiated cell

TRACHEA (*pl.* **TRACHEAE**). An air tube; specifically, the air passage from the larynx to the bronchi in vertebrates, or a part of the breathing system in tracheate arthropods.

TRANSFORMATION OF ENERGY. The process of changing potential energy (energy of configuration or position) into kinetic energy (energy of motion), or the reverse process; in cells, potential energy is stored in the complex chemical molecules and released, or transformed, by the disintegration of these into simpler molecules; the transformation of potential into kinetic energy is always accompanied by the production of heat; the activities of organisms are dependent on the release of kinetic energy.

TRIPLOBLASTIC. Having three cell layers, ectoderm, endoderm, and mesoderm, a digestive cavity lined with endoderm, and usually a coelom. *Cf.* **MONOBLASTIC** and **DIPLOBLASTIC.**

TROPISM. Preferably defined as a forced reaction given to certain stimuli by sessile animals and plants, although often used as a synonym of taxis.

TRUE COELOM. *See* **COELOM.**

TYPHLOSOLE. A single, thick, dorsal invagination of the wall of the digestive tract in some invertebrates. *Cf.* **VILLUS.**

ULTRAMICROSCOPIC. Too small to be seen with a light microscope.

UMBILICAL CORD. A cord containing blood vessels and extending from an embryo to its placenta.

UMBO (*pl.* **UMBONES**). A dome-like projection of each valve near the hinges of the shells of certain mollusks.

UNI-. Combining form, meaning "one." *Cf.* **MULTI-.**

UNIVERSAL SYMMETRY. Symmetry in any plane passing through a diameter of a spherical mass.

URINARY. Pertaining to urine.

URINO-GENITAL. Pertaining to the excretory and genital organs.

UTERUS (*pl.* **UTERI**). The expanded portion of an oviduct in which zygotes develop.

VALVE. Any part of an organism that resembles a hinged door; specifically, thin folds that control the direction of flow of blood and lymph, and the parts of the shell of pelecypods and brachiopods.

VARIATION. The lack of resemblance between the individuals of a species; may or may not be heritable.

VARIETY. A subdivision of a species.

VAS (*pl.* **VASA**). *See* **VESSEL.**

VASCULAR. Pertaining to the circulation of fluids.

VEGETAL HEMISPHERE. That half of a telolecithal egg which does not contain the nucleus and is filled with yolk. *Cf.* **ANIMAL HEMISPHERE.**

VEGETAL POLE. A point on the surface of an egg opposite the animal pole; one end of the egg axis.

VEGETATIVE CELL. *See* **METABOLIC CELL.**

VEIN. A blood vessel carrying blood from capillaries toward the heart. *Cf.* **ARTERY.**

VENTRAL. Pertaining to or situated near the surface away from the back; the lower part of an animal or part; opposite to dorsal.

VENTRICLE. A hollow part or organ; a cavity; specifically, the ventricle of many hearts and the ventricles of the vertebrate brain.

VERMES. *See* **WORM.**

VERNAL. Pertaining to the spring season; as vernal ponds, vernal vegetation.

VERTEBRA (*pl.* **VERTEBRAE**). One of the ring-like segments composing the vertebral column, or backbone.

VERTEBRATE. An animal possessing a vertebral column. *Cf.* **INVERTEBRATE.**

VESICLE. Any small, sac-like structure.

VESSEL. A tube, or canal, by which a fluid is conducted; usually restricted to those carrying blood and lymph. *Cf.* **DUCT.**

VESTIGIAL. Any organ at a given stage of development that is less developed in one individual than in another is vestigial in the former; having been better developed at an earlier stage of development or in a lower organism. *Cf.* **RUDIMENTARY.**

VILLUS (*pl.* **VILLI**). A minute, finger-like projection, containing blood vessels and occurring in great numbers, as in the intestine of vertebrates. *Cf.* **TYPHLOSOLE.**

VISCERA (*sing.* **VISCUS**). The internal organs of the body; specifically, the organs surrounded by the coelom.

VISUAL. Pertaining to sight.

VITAMINS. A group of organic compounds, occurring in small quantities in certain foods and necessary for normal metabolism.

VIVIPAROUS. Giving birth to young that develop from eggs within the body of the mother and are nourished from the blood stream of the mother. *Cf.* **OVIPAROUS** and **OVOVIVIPAROUS.**

WHITE BLOOD CELL. *See* **LEUCOCYTE** and **LYMPHOCYTE.**

WORM. In popular language, any small, elongate, creeping animal; specifically, such animals as are placed in several different groups, for example, the Platyhelminthes, Nematoda, and Annelida.

X-CHROMOSOME. A sex chromosome that is paired in one sex and single in the other, where it may or may not be associated with a Y-chromosome.

Y-CHROMOSOME. A sex chromosome that occurs in only one sex, if at all, and is not paired; carries very few genes.

YOLK. Complex food material stored in a female germ cell or an associated cell and used during development.

ZOOGEOGRAPHY. The science of the distribution of animals over the surface of the earth at a given period of time. *Cf.* **PALEONTOLOGY.**

ZOOID. Any member of a colony of metazoan animals; specifically, one of the individuals of which an ectoproct or coelenterate colony is composed. *Cf.* **POLYP.**

ZOOLOGY. The science of animal life.

ZYGOTE. A cell produced by the union of two gametes.

INDEX

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